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Forest Health and Biotechnology: Possibilities and Considerations

Committee on the Potential for Biotechnology to Address Forest Health

Board on Agriculture and Natural Resources

Division on Earth and Life Studies

A Consensus Study Report of
The National Academies of
SCIENCES • ENGINEERING • MEDICINE

THE NATIONAL ACADEMIES PRESS
Washington, DC
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500 Fifth Street, NW

Washington, DC 20001

This study was supported by the U.S. Endowment for Forestry and Communities (Grant Agreement E17-49); the Agricultural Research Service (Agreement No. 59-0790-7-0018); the Animal and Plant Health Inspection Service (Agreement No. 16-2000-0094-GR), the National Institute of Food and Agriculture (Agreement No. 2017-38832-26613), and the U.S. Forest Service (Agreement No. 16-DG-11132650-299) of the U.S. Department of Agriculture; and the U.S. Environmental Protection Agency (Contract No. EP-C-14-005). Any opinions, findings, conclusions, or recommendations expressed in this publication do not necessarily reflect the views of any organization or agency that provided support for the project.

International Standard Book Number-13: 978-0-309-XXXXX-X

International Standard Book Number-10: 0-309-XXXXX-X

Digital Object Identifier: <https://doi.org/10.17226/25221>

Additional copies of this publication are available from the National Academies Press, 500 Fifth Street, NW, Keck 360, Washington, DC 20001; (800) 624-6242 or (202) 334-3313; <http://www.nap.edu>.

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Printed in the United States of America

Suggested Citation: National Academies of Sciences, Engineering, and Medicine. 2019. *Forest Health and Biotechnology: Possibilities and Considerations*. Washington, DC: The National Academies Press. doi: <https://doi.org/10.17226/25221>.

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Preface

Nearly one-third of the United States is covered by forests, accounting for more than one million square miles, an area exceeded only in Canada, Brazil, and Russia. These forest ecosystems play vital roles in carbon storage, nutrient cycling, and air and water purification, as well as in supplying habitat for wildlife. Forests hold historical, cultural, and social significance for Americans and are sources of both food and fiber. Today, these valued resources are endangered as never before. Global commerce has hastened the introduction of nonnative, invasive tree pests and diseases, and those native to the country are becoming more virulent due to external drivers such as climate change. The loss of a tree species can have cascading adverse effects on the forest ecosystem and on the range of services it provides and the values it represents to human populations.

Against this backdrop, a consortium of federal agencies asked the National Academies of Science, Engineering, and Medicine to consider the potential for the use of biotechnology to mitigate these threats to the health of the nation's forests. Accordingly, our committee took up the tasks of assessing the ecological, economic, and social implications of deployment of a genetically modified tree and of identifying the knowledge needed to evaluate the ways such a tree might affect the prospects for forest health. The circumstances of introduction of a long-lived biotech tree into a forest ecosystem would be novel compared with the use of the technology in industrial plantations or, indeed, in annual agricultural crops. The release of a tree developed to be resistant to a pest or disease would be intended to promote its survival and proliferation in a natural forest setting.

The committee's members represent an unusually wide range of disciplines, from genetics to ecology and from the law to social science and philosophy. The group embraced the holistic view set out in its charge and probed the biophysical and the cultural and social impacts that might arise from the introduction of a biotech tree. Contemplating the rapidly evolving science and emerging public views relevant to the use of biotechnology in forest trees, the committee found itself surveying a frontier of possibilities for different kinds of trees and ecosystems. The release of a biotech tree has no direct precedent, and so the committee listened to a range of voices in the scientific community and in civil society as they speculated on the likely implications of an introduction. Unease about the advisability of the use of biotechnology in the environment will continue to be a factor in public dialogue as biotech trees are considered further. As might be imagined, the committee's discussions have been lively as we have tried to accommodate a diversity of perspectives, anticipate key information needs, and chart the way forward for researchers, government scientific and regulatory officials, and society at large.

None of the work the committee has done would have been possible without the stalwart support of Kara Laney, study director, and Jenna Briscoe, research assistant, of the Board on Agriculture and Natural Resources. Kara has been a gracious and steadying presence as we have tried to meld our disparate thoughts into a cohesive narrative. In our meetings, Jenna was a wizard when it came to listening to our fragmented discussion and transforming it instantly into text that we could see and use to move deliberations forward. All of the members of our committee have invested significant time and energy in meeting the challenge of our task, and I am grateful for their dedication. I have learned much from their expertise and their wisdom, and I am the better for it. Finally, thanks go to those who reviewed our draft report and provided comments and advice that have made it a better product for our sponsors and for the public concerned with the future of America's forests.

Susan E. Offutt, *Chair*
Committee on the Potential for Biotechnology
to Address Forest Health

Acknowledgments

This Consensus Study Report was reviewed in draft form by individuals chosen for their diverse perspectives and technical expertise. The purpose of this independent review is to provide candid and critical comments that will assist the National Academies of Sciences, Engineering, and Medicine in making each published report as sound as possible and to ensure that it meets the institutional standards for quality, objectivity, evidence, and responsiveness to the study charge. The review comments and draft manuscript remain confidential to protect the integrity of the deliberative process.

We thank the following individuals for their review of this report:

Sally N. Aitken, University of British Columbia
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Daniel Simberloff, University of Tennessee

Although the reviewers listed above provided many constructive comments and suggestions, they were not asked to endorse the conclusions or recommendations of this report nor did they see the final draft before its release. The review of this report was overseen by **May R. Berenbaum**, University of Illinois at Urbana-Champaign. She was responsible for making certain that an independent examination of this report was carried out in accordance with the standards of the National Academies and that all review comments were carefully considered. Responsibility for the final content rests entirely with the authoring committee and the National Academies.

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Selected Acronyms and Abbreviations

APHIS	Animal and Plant Health Inspection Service
<i>Bt</i>	<i>Bacillus thuringiensis</i>
CFR	Code of Federal Regulations
CRISPR	Clustered Regularly-Interspaced Short Palindromic Repeats
EA	Environmental Assessment
EAB	emerald ash borer
EIS	Environmental Impact Statement
EPA	U.S. Environmental Protection Agency
FDA	U.S. Food and Drug Administration
FFDCA	Federal Food, Drug, and Cosmetic Act
FIFRA	Federal Insecticide, Fungicide, and Rodenticide Act
FONSI	Finding of No Significant Impact
FWS	Fish and Wildlife Service
HERA	Human Health and Ecological Risk Assessment
Mbp	megabase pair
NEPA	National Environmental Policy Act
OxO	oxalate oxidase
QTL	quantitative trait locus
PERAL	Plant Epidemiology and Risk Assessment Laboratory
PIP	Plant-Incorporated Protectant
RNAi	RNA interference
USDA	U.S. Department of Agriculture

Summary

Between the 18th century and the first half of the 20th century, forest ecosystems in eastern North America lost an iconic tree species, the American chestnut, to two introduced pathogens. The loss of the chestnut (an estimated 4 billion trees) to chestnut blight and root rot caused adverse effects on other species and disrupted livelihoods dependent on chestnut products. During the same time period, white pine blister rust decimated white pines in the western United States. In the early 21st century, most eastern North American species of ash began succumbing to an insect pest introduced from Asia, the emerald ash borer. Losses in the form of timber value and removal of urban trees made the borer a costly forest pest. Some species of native bark beetles have killed billions of trees since 1990 in the West. These are just a few of the North American tree species that have been functionally lost or are in jeopardy of extirpation due to insect pest and pathogen outbreaks. The Forest Service of the U.S. Department of Agriculture (USDA) estimates that 32.9 million hectares (81.3 million acres)—that is, almost 7 percent of all forested¹ or treed² land in the United States—are at risk of losing at least 25 percent of tree vegetation between 2013 and 2027 due to insects and diseases (see Figure S-1).

Outbreaks of native pests are common disturbances in forests and can be integral to renewing forest ecosystems and maintaining biodiversity. However, ecosystems can be seriously disrupted when a nonnative, invasive pest³ is introduced or when native pests increase their geographic range or become more virulent because of external drivers such as climate change. Massive, synchronous die-offs threaten the survival of tree species and negatively affect ecosystem services, such as water filtration, soil erosion prevention, carbon sequestration, livelihoods, and social values.

Effects of pest outbreaks could be mitigated through preventing arrival of invasive species, site management practices, biological control agents, the use of genetic resistance naturally present in target species, or biotechnological modifications to confer resistance in the target species. As of 2018, American chestnut and hybrid poplars were the only two tree species on which biotechnology had been used for forest health purposes in the United States, and these trees were still in field trials. Given the threats to North American forests, USDA,⁴ the U.S. Environmental Protection Agency (EPA), and the U.S. Endowment for Forestry and Communities asked the National Academies of Sciences, Engineering, and Medicine to convene a committee of experts to investigate a number of questions related to the potential for biotechnology to be used in trees to address forest health (see Box S-1). The committee was not asked to examine the potential for biotechnology to reduce threats to forest health by altering the pests affecting North American tree species.

¹Forested land contains at least 10 percent tree canopy cover.

²Treed land is an area with measurable tree presence, including urban areas and land in the Great Plains with trees that does not meet the definition of forested land.

³The general term *pest* includes both insects and pathogens that cause damage to forests.

⁴The specific sponsoring agencies within USDA were the Agricultural Research Service, Animal and Plant Health Inspection Service, U.S. Forest Service, and National Institute of Food and Agriculture.

BOX S-1 Statement of Task

An ad hoc committee will examine the potential use of biotechnology for mitigating threats to forest tree health; identify the ecological, economic, and social implications of deploying biotechnology in forests; and develop a research agenda to address knowledge gaps about its application. The study will focus on trees and consider at least two cases that consider the use of biotechnology to protect a tree species from an insect and/or disease where negative consequences for forest health are anticipated. It will be guided by the following questions:

1. What is the current state of the science regarding the potential for using genetic engineering (GE) and similar technologies in trees to improve forest health?
2. What are the potential ecological and economic impacts of deploying trees protected from pests and pathogens using biotechnology?
3. What other unique challenges and opportunities are posed by the development of a GE product for a noncommercial, public good such as forest health?
4. What research is needed to fill knowledge gaps about developing and using GE as a tool to protect forest health?
5. In what ways does the current regulatory system include forest health in evaluating the ecological and environmental risks of deploying trees developed with GE, and how does this compare with regulatory evaluation of impacts for other methods used to address forest health threats such as non-GE trees or other biological control or pesticide approaches?
6. What information or analysis is needed to inform a risk framework that provides assurances for minimizing the risks of using GE while increasing benefits to forest health; for example, what characteristics of forest health are central to a risk framework? How can adaptive management be used to enable realistic testing and assessment of biotechnology approaches for mitigating threats to forest health?
7. What does existing research reveal about public views on the use of biotechnology to improve forest health?

The committee will prepare a report that addresses the questions above and explains the basis for its conclusions and recommendations.

THE COMMITTEE'S PROCESS

Members of the Committee on the Potential for Biotechnology to Address Forest Health were appointed by the president of the National Academy of Sciences for their expertise in a variety of disciplines pertinent to the study's task. To help it address that task, the committee held information-gathering meetings between December 2017 and April 2018. It heard from 43 speakers during three in-person meetings and 10 webinars. The committee also reviewed the scientific literature and welcomed comments by members of the public. The committee used this information-gathering process to define forest health and to shape its report (see Box S-2). The conclusions and recommendations included in the summary are based on the main body of the committee's report.

THREATS TO FOREST HEALTH FROM INSECT PESTS AND PATHOGENS

Since the 1600s, around 450 species of insects and at least 16 species of pathogens have been introduced and become established in continental U.S. forests. Of those, 62 insects and all of the pathogens have been classified as high-impact species, causing some combination of tree mortality, canopy thinning, growth loss, defoliation, and decreased reproduction or regeneration. Some of these introductions have had devastating consequences in North American forests; impacts have ranged from temporary declines in population productivity to the functional extirpation of an entire species, as was the case with the American chestnut.

BOX S-2 Forest Health and Ecosystem Services

The committee defined *forest health* as:

A condition that sustains the structure, composition, processes, function, productivity, and resilience of forest ecosystems over time and space. An assessment of this condition is based on the current state of knowledge and can be influenced by human needs, cultural values, and land management objectives.

A healthy forest—that is, one that sustains the components of an ecosystem over time and space—is more likely to sustain ecosystem services of value to individuals and society. *Ecosystem services* are the goods and services that are of value to people, provided wholly or in part by ecosystems. They include ecological processes such as soil formation and retention, water filtration, and climate regulation as well as cultural services such as cultural heritage or identity and aesthetic values. Alongside the services they provide to humans, forest ecosystems may also be thought to have *intrinsic* value: value for their own sake.

With warmer climate, many native and nonnative insects are colonizing regions that previously had been unsuitable. Forecasts of future climate indicate likely changes in pathogen overwintering survival, changes in host susceptibility to pathogen attack due to other stressors (e.g., drought or storm damage), or changes of life cycles of insects that disperse pathogens. Changes in climate are also predicted to increase the frequency and magnitude of pest outbreaks in the future.

The effects of pests on individual trees have cascading impacts on populations, reducing reproduction and survival. Local extirpation of the tree species and extinction of species dependent on it may result. For example, five moth species went extinct with the loss of the American chestnut. Such species-specific effects can change community assemblage and structure, and thus, ecosystem function.

Conclusion: Healthy forests provide valuable ecosystem services to humans.

Conclusion: The health of North American forests is threatened by the introduction and spread of nonnative insects and pathogens and the epidemics of native pests exacerbated by environmental stress due to climate change.

Conclusion: Tree species in forest ecosystems, tree plantations, and urban landscapes across North America are threatened by insect pests and pathogens.

Conclusion: Many forest tree species are threatened by more than one insect pest or pathogen.

Conclusion: As the frequency of insect and pathogen outbreaks increases, many forest tree species are in jeopardy of being lost from the landscape, resulting in changes to ecosystem services.

MITIGATING THREATS TO FOREST HEALTH

There are multiple options for dealing with forest pests, but feasibility and success vary widely. For nonnative insects and pathogens, the first line of defense is preventing their introduction. When introduced pests have become established or native pests are expanding their range or increasing in virulence, chemical or biological control can suppress pest populations in some cases, but these approaches are often not acceptable to the public, effective, or timely. Other management practices such as quarantines or thinning tree stands may help minimize a pest outbreak but are most likely insufficient.

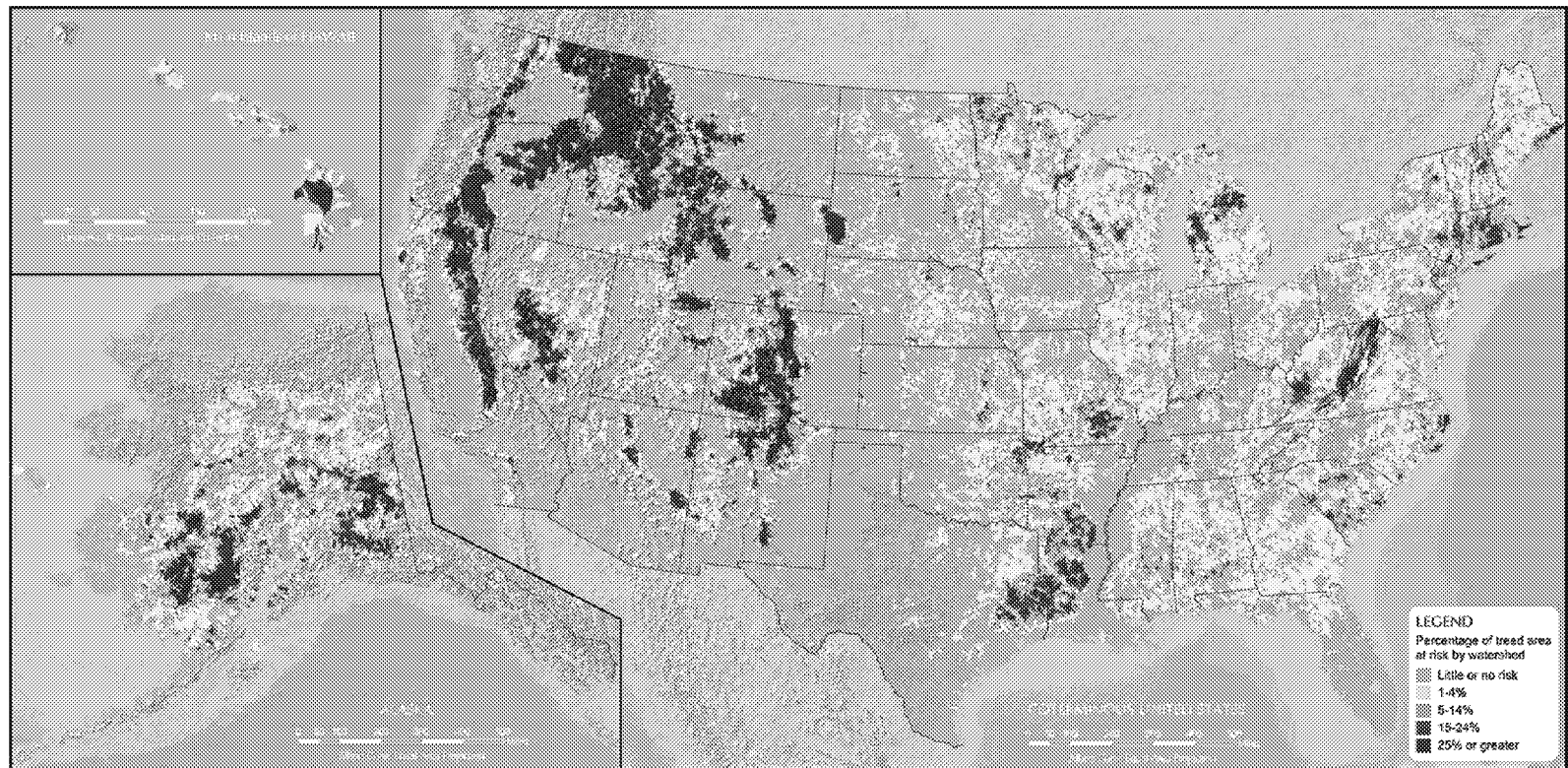


FIGURE S-1 Risk assessment from insect pests and diseases in U.S. forests by subwatershed, 2013–2027. NOTE: Hectares at risk total 32.9 million (81.3 million acres). SOURCE: Krist, F.J., J.R. Ellenwood, M.E. Woods, A.J. McMahan, J.P. Cowardin, D.E. Ryerson, F.J. Sapio, M.O. Zweifler, and S.A. Romero. 2014. 2013–2027 National Insect and Disease Forest Risk Assessment. Fort Collins, CO: U.S. Forest Service.

Trees genetically resistant to a pest have the ability to minimize or overcome the damaging effects of a pest. Genetic resistance can be accomplished through selective breeding or biotechnology. The first step in selective breeding is to determine whether genetic resistance exists within the affected species population. Finding suitable parent trees can be difficult, and even with resistant parent trees, not all of the progeny will be resistant. Evaluating the durability of resistance will also be paramount because trees will be on the landscape for decades. Resistant progeny will need to be propagated in greenhouses or seed orchards to create sufficient resistant genotypes for restoration and reforestation.

To use biotechnology to confer resistance, the first step is to identify genes for modification, introduction, or silencing. If a gene is not already in hand, then a gene discovery process is required. This step has been hindered due to trees' large size, long generation time, and (in the case of conifers) immense genomes. Another problem is that forest trees have high levels of heterozygosity due to their large population sizes and outcrossing breeding systems, which complicates genome assembly and modification.

The second step is production of trees containing the desired gene sequence. Biotechnology tools such as transgenesis and genome editing, used to introduce a desired change to gene sequence, are followed by tissue culture protocols, in which the desired gene can be introduced into a single cell. Then whole plants are generated from the transformed cell by regeneration of roots and shoots from disorganized callus tissue. However, many species of trees remain recalcitrant to cell culture and regeneration. Even when possible, the regeneration of a plant from a single cell may not produce an individual that has the desired genetic change in every cell.

Thus, using biotechnology to introduce traits to address forest health has its challenges. Nonetheless, biotechnological research to introduce or modify traits in trees has been explored in a number of tree species since the late 1980s. For a forest health threat, the most advanced research has been conducted on the American chestnut. A wheat gene encoding the enzyme oxalate oxidase (OxO) has been inserted into the chestnut genome using transgenesis. Oxalic acid generated by the chestnut blight weakens cell walls, enabling other fungal enzymes to degrade the wall and cell membranes, killing the cell. Widespread cell death eventually girdles the tree. The OxO enzyme expressed in transgenic chestnut converts oxalic acid to carbon dioxide and hydrogen peroxide, thereby conferring on the tree genetic resistance to the blight.

Conclusion: Substantial literature supports the need for sustained investment in prevention and eradication as the most cost-effective and lowest impact approaches for managing introduction of nonnative insect pests and pathogens.

Recommendation: Investment in effective prevention and eradication approaches should be the first line of defense against nonnative species in efforts to maintain forest health.

Conclusion: Any single management practice alone is not likely to be effective at combatting major pest outbreaks.

Recommendation: Management for forest health should make use of multiple practices in combination to combat threats to forest health.

Conclusion: A variety of biotech and nonbiotech approaches have been and will be developed to address insect pest and pathogen threats. The time line for use of these tools in management activities for forest trees and forest health will depend on a number of factors, but the biology of the species involved (both tree and insect or pathogen) and the environments in which the tree species exist will have a major influence on effective mitigation.

Conclusion: Many tree species have some degree of resistance to particular native and nonnative pests that may be harnessed to combat infestations and epidemics.

Recommendation: Entities concerned about forest health should devote resources to identifying resistant trees within a population that have survived a pest outbreak. Research to understand the role of resistance in coevolved systems from the perspective of a global host–pest system, where the nonnative pathogen or insect originate, would help guide efforts in North America.

Conclusion: Using biotechnology to introduce resistance to threats in forest trees has been hampered by the complexity of tree genomes, the genetic diversity in tree populations, and the lack of knowledge about genetic mechanisms that underlie important traits. However, recent technological developments have improved functional genomic tools, facilitating the potential for biotechnology to help address forest health problems.

Recommendation: More research should be conducted on the fundamental mechanisms involved in trees' resistance to pests and adaptation to diverse environments, including a changing climate.

Conclusion: The time it takes to identify resistance in an affected population, breed resistant seedlings, and plant resistant seedlings in the field can vary from a few years to multiple decades, depending on the species. Incorporating resistance via biotechnology into a tree species is also a lengthy process, the duration of which varies by species.

Recommendation: Sufficient investment of time and resources should be made to successfully identify or introduce resistance into tree species threatened by insects and pathogens.

CONSIDERATIONS RELATED TO THE USE OF BIOTECHNOLOGY IN FOREST TREES

Any intervention to address forest health involves consideration of associated ecological, economic, social, and ethical issues. Some of these considerations are unique to biotechnology, but others are applicable to any intervention.

Several ecological considerations arise in evaluating the use of biotechnology to maintain or improve forest health. They include whether there will be potential gene flow from the biotech tree to relatives and, if so, whether there will be an effect on other species in the environment. Additionally, interspecies gene flow, via horizontal gene transfer or hybridization, could also occur. Genetic fitness of modified trees will be critical because the intent of biotech trees is to recover species over large temporal and spatial scales. Furthermore, even if a biotech tree is genetically fit and able to convert its resistance to subsequent generations, it will not become established in a forest if it is not competitive in the ecosystem.

Genetic variation in trees also needs to be considered in restoration efforts so that modified trees are suited for the environment in which they are planted. An important difference in forest trees versus agricultural uses of biotechnology is that a focus on recovering forest species requires incorporating the specific genetic change while retaining the breadth of genetic diversity in forest populations. This diversity permits the species to continue to evolve under changing abiotic and biotic conditions. In particular, understanding the patterns of radiation out of the glacial refugia (i.e., geographic regions where flora and fauna survived during the ice ages and later recolonized postglacial habitats) and how that has shaped the standing genetic variation in response to past climates is important when choosing genetic backgrounds against which to deploy biotechnological solutions to climate or pest mitigation.

Trees, once planted and maturing, can provide both public and private benefits. Public benefits are those that cannot be exclusively captured by an individual or a firm but are shared across many people and communities. The costs of development of a biotech tree will be incurred up front and the benefits will follow years later. Such a difference in the timing makes investment with a long time horizon problematic. Compared to the private sector, the public sector can have greater patience when significant public benefits are forthcoming. The economic argument for a public-sector role also arises out of the likelihood that the private sector will not invest in the protection of forest health because it cannot fully capture the benefits that may accrue.

Public opinion research suggests that people generally have positive attitudes about the use of biotechnology in forests, although they often prefer nonbiotech interventions if given the choice. In addition, some biotechnological interventions (e.g., cisgenic or within-species interventions) are sometimes preferred by the public over others (e.g., transgenic or between-species interventions). However, many people lack detailed knowledge of these interventions, such as the processes used in any intervention. As various publics increase their familiarity with this topic, attitudes, norms, and perceptions of risks and benefits may change. Societal responses are highly dynamic, contextual, and varied in their intensity.

Developing biotechnology for use in trees and forests raises a range of social and ethical considerations. Some directly relate to the provisioning of ecosystem services, including the perceived benefits to people and the environment, but others include intrinsic value, wildness, broad social influences, and social justice concerns.

Biotechnology intended to influence and alter the forest could be interpreted as a form of human control of a forest ecosystem. Transgenic or genome-edited trees, planted and possibly managed and monitored by humans, could be understood to reduce wildness. The use of biotechnology is also a human intervention in the “natural” evolutionary trajectory of the forest. Although the use of biotechnology may promote forest health, it may be perceived as diminishing the forest’s wildness. On the other hand, *threats* to forests that biotechnology may counter are predominantly of human origin (e.g., invasive pests transported by people and native pests extending their range because of human influences on climate). Given that these changes are also signs of human influence, forest wildness may *already* be seen as reduced. Doing nothing to counter such threats may result in the loss of populations or entire species, with significant effects on forest ecosystems that also mean a loss of wildness. Other practices that might address forest health, such as selective breeding, pose similar threats to wildness because they involve the selection of genotypes, the decision to plant trees, and continued monitoring of the trees.

Conclusion: Trees with resistance introduced via biotechnology will have to survive until maturity and reproduce in order to pass resistant traits on to the next generation.

Recommendation: Research should address whether resistance imparted to tree species through a genetic change will be sufficient to persist in trees that are expected to live for decades to centuries as progenitors of future generations.

Conclusion: The importance of managing and conserving standing genetic variation to sustain the health of forests cannot be overstated.

Recommendation: The deployment of any biotechnological solution with the goal of preserving forest health should be preceded by developing a reasonable understanding in the target species of (a) rangewide patterns of distribution of standing genetic variation including in the putative glacial refugia, if known; (b) magnitude of local adaptation (*gene × environment* relationships); and (c) identification of spatial regions that are vulnerable to genetic offset.

Conclusion: The public sector will be best positioned to lead development of biotech trees because of the public-good aspect of forest health and the intention for the spread of a biotech tree through a forest ecosystem.

Conclusion: The relatively long time required for the development of a biotech tree may adversely affect the incentive for both private- and public-sector investment.

Conclusion: Few studies of public attitudes toward biotechnology to address forest health threats have yet been carried out in the United States. However, there has been a small handful of studies on the topic, especially in Canada and Europe. The limited data indicate that while some individuals

and groups are very concerned about possible deployment of biotechnology in forests, attitudes toward the uses of biotechnology examined in these studies are somewhat positive, especially where threats to forests are severe.

Conclusion: Existing research indicates that public knowledge and understanding about the use of biotechnology in forests is low, suggesting that current attitudes may be unstable and liable to change with more information. The power of such information to influence attitudes is mediated by the perceived trust of the sources of information, deliberation about the topic, as well as the alignment of new information with deep value orientations.

Conclusion: Some important ethical questions raised by deploying biotechnology in noncommercial forests fall outside any evaluation of changes in ecosystem services.

Recommendation: More studies of societal responses to the use of biotechnology to address forest health threats in the United States are needed. Such studies might investigate (1) the responses of different social and cultural groups to the deployment of biotechnology in forests, (2) the stability and consistency of attitudes toward different applications of biotechnology in a range of circumstances, (3) differences in attitudes toward biotechnology strategies (e.g., cisgenesis, transgenesis, genome editing), (4) the relationship between deeper value orientations and attitudes toward biotechnology, and (5) how people consider trade-offs between values such as wildness and species protection.

Conclusion: The use of biotechnology for forest health, especially in noncommercial forests, raises broad questions about the social impacts of technological change on society, in particular how conservation is understood and practiced, and how far biotechnological interventions presage a change to more interventionist management of forests.

Conclusion: The use of biotechnology for forest health raises social justice questions, both in terms of the distribution of risks, harms, and benefits across individuals and groups through time and in terms of the procedures used to make decisions about whether, when, and where to deploy the technology. Indigenous communities may be particularly affected by these decisions. Given the longevity of trees, the use of biotechnology for forest health (or the decision not to use it) will have significant impacts on future generations.

Recommendation: Respectful, deliberative, transparent, and inclusive processes of engaging with people should be developed and deployed, both to increase understanding of forest health threats and to uncover complex public responses to any potential interventions, including those involving biotechnology. These processes, which may include surveys, focus groups, town hall meetings, science cafés, and other methods, should contribute to decision making that respects diverse sources of knowledge, values, and perspectives.

INTEGRATED IMPACT ASSESSMENT FRAMEWORK

When assessing the impact of a pest threat on forest health, evaluating the effect of that threat on forest processes and cultural and spiritual values provides the basis for assessing how the provision of ecosystem services may change. The risk of loss of ecosystem services over part, or all, of a species' range is weighed against the potential to recover ecosystem services with and without the biotech intervention. Such a framework could be used to evaluate any forest health intervention, including the use of selectively bred trees.

When considering impact assessment for the use of biotechnology in forests, links between specific forest protections and their effects on important ecosystem services should be made explicit. Existing EPA guidance on classification and measurement of ecosystem services provides a useful frame that can be

modified to address the range of services provided by introduction of pest-resistant trees. The advantage of bringing ecosystem services into impact assessment is that it makes possible the inclusion of a broader range of values and the connection between the protection of forests and human well-being clear for the public, stakeholders, and policy makers.

At the time the committee was writing its report, few biotech trees developed to address forest health had been planted in field conditions; those that had were still in field trials. Because of the length of time until tree reproductive maturity and long life span of most trees, collecting data for an impact assessment may take years to compile. To help address this issue, data from field trials can be combined with data derived from other types of biotech plant releases to parameterize simulation models to inform impact assessment. Modeling approaches can include gene flow and climatic tolerances. Surveys and stakeholder engagement will help to identify human values and concerns associated with specific products of biotechnology. Synthesis of all available information will aid in making informed predictions of potential risks. Modeling scenarios that include sources of uncertainty will allow quantification of the reliability of the assessments, estimation of the predictive capacity of the model, and identification of data needs.

Coupling adaptive management with impact assessment would allow adjustments to be made to decisions about the development and deployment of biotech trees for forest health as data are collected. However, the ability to make adjustments based on new knowledge is complicated by the U.S. regulatory system, which generally does not permit the flowering of biotech trees. Without flowering, it is difficult to gather data on gene flow and other parameters to inform an impact assessment framework. A hierarchical regulatory system that assigns biotech trees to different tiers of risk would be more amenable to adaptive management. If data on gene flow and impacts on ecosystem services were simultaneously collected, they could be used to refine simulation models to obtain more precise prediction of potential outcomes. These analyses could then be used to propose increasingly larger environmental releases until the trees are either discontinued or deregulated by the relevant oversight agency. This stepwise approach may be the only practical way to obtain data on gene flow and impacts at the spatial and temporal scales that are needed for proper impact assessment for biotech trees.

Conclusion: An integrated impact assessment framework that combines ecological risk assessment with consideration of ecosystem services would provide a way to evaluate impacts of introduction of a biotech tree both on the forest functions and on the ecosystem services provided. Societal and cultural values need to be incorporated into this approach.

Recommendation: Federal agencies should continue efforts to improve the incorporation of all components of ecosystem services into the integrated impact assessment.

Conclusion: Field trials are an important tool to gather data on biotech trees in terms of gene flow, the durability and effectiveness of resistance, seed generation and dispersal, genetic fitness, and some impacts on the ecosystems into which the trees are planted.

Conclusion: Modeling efforts will be essential to address the large spatial and temporal scales and stochastic nature of biotech tree impact assessment.

Recommendation: Modeling and other approaches should be developed to address questions about biotech tree gene flow, dispersal, establishment, performance, and impact that are precluded where flowering of field trial material is restricted.

Recommendation: Models for tree biotech impact assessments should identify, quantify, and account for sources of uncertainty.

Conclusion: Iterative decision making is required, such that impact assessments are continually modified with improvements in knowledge gained through on-the-ground experience with biotech tree

development, testing, and deployment because of the uncertainty associated with predictions of the impacts of release of biotech trees into minimally managed or unmanaged environments.

Recommendation: An adaptive management approach to forest health should be used to ensure continued learning and address impacts to both the environment and society.

Recommendation: Impact assessment should be a continuous and iterative process.

U.S. REGULATORY SYSTEM AND FOREST HEALTH

Biotech trees developed to address forest health are regulated under the same statutes and regulations as any biotech plant. The Coordinated Framework for the Regulation of Biotechnology, established in 1986, specified that oversight of biotechnology products would be carried out using existing legislative statutes. Under the framework, up to three federal agencies—USDA, EPA, and the U.S. Food and Drug Administration—are most likely to have a role in the regulatory oversight of a biotech tree developed to address forest health.

The statutes utilized by these agencies do not consider most aspects of forest health in analyzing the safety of a biotech plant. The different statutes grant each agency authority to regulate specific products, not the process by which the products are produced. The application of the Coordinated Framework to specific products means that biotech trees and plants may be regulated by zero, one, two, or three or more agencies.

Forest health also is not considered in the regulation of nonbiotech products designed to address forest health problems. The assessments or reviews conducted for these management options do not do a better job of incorporating forest health and ecosystem services into their analysis than the assessments conducted for biotech trees.

Conclusion: The current regulatory framework for biotech plants applies to biotech forest trees and does not impose any additional or different requirements for trees than other plants.

Conclusion: The current regulatory framework that applies to biotech trees that are developed to address forest health encapsulates very few elements of the committee's comprehensive definition of forest health.

Conclusion: If a regulatory agency is required to comply with the National Environmental Policy Act (NEPA) when regulating a biotech tree, then some components of forest health will be analyzed.

Conclusion: USDA only carries out a NEPA analysis—environmental assessment and/or environmental impact statement—for a small subset of biotech trees.

Conclusion: As is the case with other biotech plants, some biotech trees could become commercial products without any oversight by the three regulatory agencies.

Conclusion: There are mechanisms in place to alert neighboring countries about biotech forest trees that could enter their territory, but biotech trees could migrate across a national border without notice if the biotech tree is not regulated in the country of origin.

Conclusion: Forest health also is not considered in the regulation of nonbiotech products designed to address forest health problems, such as biological control agents, pesticides, and assisted migration.

Conclusion: Some federal agencies have policies for the assisted migration of trees and/or the planting of biotech trees on federal lands while private landowners can plant nonnative and biotech trees without violating any federal laws or policies.

Recommendation: Regulatory agencies should explore ways to incorporate into their regulatory oversight responsibilities the ability to assess the impact on ecosystem services for both biotech and nonbiotech products developed for improving forest health.

MOVING AHEAD

Biotechnology has the potential to help mitigate threats to North American forests from insect pests and pathogens through the introduction of pest-resistant traits. However, it also presents some challenges. The necessary genetic changes to achieve resistance are often not easy to identify and are challenging to incorporate. Tree genomes are complex, and much remains to be learned about the genetic mechanisms that underlie important traits. Additionally, unlike the modification of agricultural crops through biotechnology—in which a genetic change is introduced to and propagated in an individual variety—genetic changes in trees for forest health purposes need to be introduced into diverse breeding populations so that tree species can respond to biotic and abiotic stress over time and across their spatial distributions.

Furthermore, the effectiveness of biotechnology at mitigating forest threats needs to be assessed on many fronts. In addition to evaluating the utility of the resistance trait in protecting a tree species, the modified tree needs to be tested for viability in the diversity of environments in which it will live. An assessment of the effects of the tree on other species in the environment is also important, as is a comparison of using biotechnology to address the threat versus other mitigation tools.

Finally, research and investment efforts need to be made in areas besides biotechnology, including the development of further strategies for preventing the introduction of nonnative insects and pathogens, human capital development in professions related to tree breeding, and social science research, including a conceptual framework for capturing and accounting for the intrinsic value of forests. Such work will benefit the health of forests, regardless of the pest mitigation tools put to use.

Therefore, the committee's preceding recommendations point toward research and investment on three fronts that would (a) address knowledge gaps about the application of biotechnology to mitigate threats to forest health and (b) improve the utility of biotechnology as a forest health tool:

1. Knowledge about tree genetics related to resistance, specifically investment in identifying resistant trees in populations that have survived pest outbreak and research on the fundamental mechanisms of resistance, existing genetic variation in tree populations, and the durability of resistance.
2. Data and tools for impact assessment, in particular investment in efforts to improve the incorporation of all ecosystem services into integrated impact assessments, to collect data to inform and improve models, and to increase the use of adaptive management to address forest health threats.
3. Management approaches that take into account disciplines beyond biotechnology, including more studies on societal responses to using biotechnology to address forest health, more investment in prevention and eradication efforts of introduced pests, and better efforts at respectful, deliberative, transparent, and inclusive processes of engaging with people to increase understanding of forest health threats and to uncover complex public responses to potential interventions.

Additionally, the committee includes the following recommendations to support a holistic effort to improve forest health with the help of biotechnology.

Recommendation: Public funders should support and expand breeding programs to encompass the genetic diversity needed to preserve tree species essential to ecosystem services.

Recommendation: Investment in human capital should be made in many professions, including tree breeding, forest ecology, and rural sociology to guide the development and deployment of pest-resistant trees.

Recommendation: Studies of societal responses to the use of biotechnology to address forest health threats should be used to help in developing a complementary framework to ecosystem services that takes into account intrinsic values, related spiritual and ethical concerns, and social justice issues raised by the deployment of biotechnology in forests.

Recommendation: Developers, regulators, and funders should experiment with analytical-deliberative methods that engage stakeholders, communities, and publics.

Introduction

Between the 18th century and the first half of the 20th century, forest ecosystems in eastern North America lost an iconic tree species, the American chestnut, to two introduced pathogens. The lower elevation southern portions of the American chestnut range experienced high mortality from root rot beginning in the 18th century, while the chestnut blight arrived from Asia in the late 1800s and devastated chestnut throughout its range into the 20th century. As a foundational species in the ecosystems it inhabited, the loss of the American chestnut (an estimated 4 billion trees) to chestnut blight and root rot caused a cascade of adverse effects on other species and disrupted livelihoods in communities that depended on chestnut products. During the same time period, white pine blister rust decimated many populations of white pines in the western United States; one of the affected species, whitebark pine, has been proposed for listing under the Endangered Species Act. In the early 21st century, most of the eastern North American species of ash began succumbing to an introduced insect pest, the emerald ash borer. Losses in the form of timber value and removal of urban trees made the borer a costly forest pest (Poland and McCullough, 2006; Kovacs et al., 2010; Hauer and Peterson, 2017). In some of the largest insect outbreaks ever recorded, a few species of native bark beetles have killed billions of spruce, fir, and pine trees since 1990 in the North American West. The most common native tree in Hawai'i, the 'ōhi'a, has been severely affected by a fungal disease first detected in 2015. These massive, synchronous die-offs threaten the survival of these tree species on the landscape and negatively affect the ecosystem services provided by the living forests, such as water filtration, soil erosion prevention, carbon sequestration, livelihoods, and other social values.

These are just a few of the North American tree species that have been functionally lost or are in jeopardy of being extirpated from the environment due to insect pest and pathogen outbreaks. Outbreaks of native pests are common disturbances in forests, occurring across ecosystems and landscapes, and they account for a large proportion of tree mortality in North American forests (Krist et al., 2014; Kautz et al., 2017). These outbreaks can be integral to the functioning of forests and often renew ecosystems and contribute to the creation of temporal and spatial heterogeneity, which are critical for the maintenance of high levels of biodiversity (Perry, 1994; Barnes and Wagner, 2004).

However, ecosystems can be seriously disrupted when a nonnative, invasive pathogen or insect is introduced or when native pathogens or insects increase their geographic range or become more virulent because of external drivers such as climate change. Since 1860, North American forests have experienced an increase in the frequency and magnitude of outbreaks (Boyd et al., 2013) due to an increase in global trade and travel (Early et al., 2016) and the acceleration of climate change (Dukes et al., 2009). Of the more than 60 introduced insect species known to be established and to cause damage in continental U.S. forests, only two were detected before 1860 (Aukema et al., 2010). Of the 16 pathogens known to be introduced, all adversely affect North American forests (Aukema et al., 2010).

The impacts of introduced forest pests¹ are being aggravated by climate change, which is expanding environmental conditions favorable for insect pests and pathogens, both native and introduced. Warmer winters, fewer days with extremely low temperatures, and longer warm seasons are simultaneously facilitating insect range expansion, local population growth, and reduced time between generations (Bentz et al., 2009, 2010; Sambaraju et al., 2012; Weed et al., 2013). Insect pests are moving higher in latitude and

¹The general term *pest* includes both insects and pathogens that cause damage to forests.

elevation (Berg et al., 2006), and cold areas that previously did not experience the population explosions associated with outbreaks have now become more favorable to such dynamics (Raffa et al., 2013). Similarly, some tree pathogens, such as *Phytophthora cinnamomi* (which causes root rot and dieback of thousands of species worldwide), are expected to expand their geographic ranges in response to climate change (Bergot et al., 2004).

In many cases, native trees may have little or no natural resistance to withstand insect or pathogen attack and are at risk of being extirpated. The decrease in abundance, or disappearance, of a tree species affected by outbreaks can in turn affect other species and trophic levels (Ford et al., 2012) and potentially result in a cascade of changes with profound impacts on the entire ecosystem (Ellison et al., 2005a,b; Morin and Liebhold, 2015) and the services it provides to humans and other species (Lewis and Lindgren, 2000; Fissore et al., 2012; Liebhold et al., 2017).

Many tools are available to mitigate the effects of insect and disease outbreaks. For introduced species, the most cost-effective measures are those that prevent the arrival of the invasive species in the first place (Lovett et al., 2016). Eradication through chemical traps, pesticide fumigations, and manual removal can eliminate small populations that are accidentally introduced (Sharov et al., 2002). Insecticides and fungicides may be used to some extent in forests even if eradication is not possible. Thinning tree stands or taking actions to promote diversity of tree species and age classes can reduce opportunities for native or introduced pests to spread (Jactel et al., 2012; DeRose and Long, 2014), and biocontrol measures—such as the introduction of predators of a damaging insect or the release of sterile insects to breed with the damaging population—may help regulate the insect pest population at lower levels (Bauer et al., 2014). Another approach is to exploit the natural genetic resistance within the affected tree species by identifying genotypes of the tree resistant to the insect or pathogen, then selectively breeding resistant trees, and ultimately introducing those bred trees into forests to continue the spread of the resistant phenotype in the forest tree population (Woodcock et al., 2017). When little or no resistance is found within a native tree species, breeding a native species with a related resistant species can be used to impart resistance.

Resistant trees can also be created through the use of biotechnology. This process may consist of inserting DNA from another tree species or an entirely unrelated species into the genome of the target tree to produce a genotype that will express resistance to the damaging insect or pathogen. The genome of the tree can also be molecularly manipulated to express resistance without the insertion of DNA from another organism. For example, many classes of chemicals are produced by forest trees that reduce herbivory and pathogen infection. Terpenes have been studied extensively in conifers and phenolics in broad-leaved trees as mechanisms of defense. However, biotechnology has significant potential to increase secondary chemical production for plant defense (Peter, 2018). Another emerging tool in the biotechnology toolkit is the synthesis of DNA—that is, DNA created in a laboratory—that can then be inserted into the genome of the tree.

As of 2018, although research on incorporating resistance to insects or pathogens via biotechnology was being conducted in some forest tree species such as the American chestnut and poplar hybrids, no such resistant genotypes—created with the intent to spread resistance into a forest population—had been planted in a North American forest. Given the increase in the frequency and magnitude of pest outbreaks, and the threats they pose to the survival of many North American forest species, a number of federal agencies and a forest organization wanted to explore whether biotechnology held potential for addressing these threats to forest health. The U.S. Department of Agriculture’s U.S. Forest Service, Animal and Plant Health Inspection Service, National Institute of Food and Agriculture, and Agricultural Research Service as well as the U.S. Environmental Protection Agency and the U.S. Endowment for Forestry and Communities asked the National Academies of Sciences, Engineering, and Medicine (hereafter referred to as the National Academies) to convene a committee of experts to investigate that question.

THE COMMITTEE AND ITS CHARGE

The committee’s charge was to examine whether biotechnology has the potential to mitigate threats to forest health, particularly threats posed by insects and diseases. Its task included identifying the ecological, economic, and social implications of using biotechnology in forests and developing a research agenda

to address areas where knowledge about such use might be lacking. The committee was instructed to use case studies to explore whether biotechnology could successfully protect forest tree species from insect pests, pathogens, or both. It was not asked to examine the potential for biotechnology to reduce threats to forest health by altering the pests affecting North American tree species. The full statement of task is in Box 1-1.

The president of the National Academy of Sciences appointed a committee with the diverse expertise and experience needed to address this statement of task. The committee contained experts in forest population genetics, tree gene flow and reproductive biology, quantitative genetics, and genomics. The disciplines of forest ecology and entomology were also represented as were the fields of sociology, ethics, economics, and U.S. environmental and regulatory law. Many committee members had extensive knowledge about selective breeding and genetic engineering of forest trees. The committee included researchers who studied conifer and deciduous trees in eastern, midwestern, intermountain, western, and Hawaiian forest ecosystems. As with all National Academies committees, members were appointed for their individual expertise, not their affiliation to any institution, and they volunteered their time to serve on this committee. The biography of each committee member can be found in Appendix A.

BOX 1-1 Statement of Task

An ad hoc committee will examine the potential use of biotechnology for mitigating threats to forest tree health; identify the ecological, economic, and social implications of deploying biotechnology in forests, and develop a research agenda to address knowledge gaps about its application. The study will focus on trees and consider at least two cases that consider the use of biotechnology to protect a tree species from an insect and/or disease where negative consequences for forest health are anticipated. It will be guided by the following questions:

1. What is the current state of the science regarding the potential for using genetic engineering (GE) and similar technologies in trees to improve forest health?
2. What are the potential ecological and economic impacts of deploying trees protected from pests and pathogens using biotechnology?
3. What other unique challenges and opportunities are posed by the development of a GE product for a noncommercial, public good such as forest health?
4. What research is needed to fill knowledge gaps about developing and using GE as a tool to protect forest health?
5. In what ways does the current regulatory system include forest health in evaluating the ecological and environmental risks of deploying trees developed with GE, and how does this compare with regulatory evaluation of impacts for other methods used to address forest health threats such as non-GE trees or other biological control or pesticide approaches?
6. What information or analysis is needed to inform a risk framework that provides assurances for minimizing the risks of using GE while increasing benefits to forest health; for example, what characteristics of forest health are central to a risk framework? How can adaptive management be used to enable realistic testing and assessment of biotechnology approaches for mitigating threats to forest health?
7. What does existing research reveal about public views on the use of biotechnology to improve forest health?

The committee will prepare a report that addresses the questions above and explains the basis for its conclusions and recommendations.

THE COMMITTEE'S PROCESS

The committee conducted its work between December 2017 and December 2018. Between December and April, it heard from 43 invited speakers over the course of 13 information-gathering sessions: three held in-person in Washington, DC, and 10 conducted via webinar. All in-person meetings and webinars were open to the public, streamed over the Internet, and recorded and posted to the study's website.² Agendas for the meetings, topics for the webinars, and names of the invited speakers can be found in Appendix B.

The committee also reviewed the scientific literature and welcomed comments submitted by members of the public. Opportunities to make public statements to the committee were available at each in-person meeting, and the committee accepted written statements throughout the study process.³ Committee members read all submitted written comments, which were subsequently archived in the study's public access file.⁴

Based on its expertise, experience, and the information it gathered through presentations, scientific literature, and written comments, the committee wrote a draft report in response to the statement of task. That draft was then reviewed by a number of peers with expertise complementary to that of the committee members in a process overseen by the National Academies' Report Review Committee. The reviewers were anonymous to the committee during the review process, and their comments remain anonymous after the report has been published (see Acknowledgments). The Report Review Committee approved the report for publication after it determined that the committee had appropriately responded to the reviewers' comments.

ORGANIZATION OF THE REPORT

The next chapter discusses the concept of forest health, including how the committee defined the term. It also reviews the threats to forest health from insect pests and pathogens, reviews the ecosystem services provided by forests, and introduces the case study species considered by the committee: American chestnut (*Castanea dentata*), whitebark pine (*Pinus albicaulis*), ash (*Fraxinus* spp.), and poplar (*Populus* spp.).

Chapter 3 outlines the options available for mitigating threats to forest health, including the current state of the science regarding the potential for using biotechnology in trees to improve forest health. The committee agreed that *biotechnology* included the following approaches: transgenesis, cisgenesis, RNA interference, genome editing, and the insertion of synthetic DNA. For simplicity's sake, trees modified by one or more of these approaches are generally referred to in this report as *biotech trees*.

Chapter 4 reviews the ecological, economic, social, and ethical considerations related to the use of biotechnology in trees. It includes a synopsis of the potential ecological and economic impacts of deploying trees protected from insect pests and pathogens using biotechnology and a summary of what existing research reveals about public views on the use of biotechnology to improve forest health.

Chapter 5 emphasizes the importance of evaluating the risk of loss of ecosystem services over part, or all, of a species' range against the potential to recover ecosystem services across that range with and without a biotechnological intervention and identifies information needs for a framework that would assess the impacts of using biotechnology to address forest health. It also explores how adaptive management could be used to test, assess, and improve the use of biotechnology as a tool to mitigate forest health threats.

Chapter 6 summarizes how forest health is considered in the U.S. regulatory systems for biotechnology and other forest health interventions. Chapter 7 describes research and investment needs to fill knowledge gaps about developing and using biotechnology as a tool to mitigate threats to forest health from insect pests and pathogens.

²Recordings of the presentations made to the committee at its meetings and webinars can be found at <http://nas.edu/forestbiotech>.

³For more information about the National Academies study process, see <http://www.nationalacademies.org/studyprocess>.

⁴The public access file of any National Academies study can be obtained by contacting the Public Access Records Office at paro@nas.edu.

REFERENCES

- Aukema, J.E., D.G. McCullough, B. Von Holle, A.M. Liebhold, K. Britton, and S.J. Frankel. 2010. Historical accumulation of nonindigenous forest pests in the continental United States. *BioScience* 60(11):886–897.
- Barnes, B.V., and W.H. Wagner. 2004. *Michigan Trees*. Ann Arbor: University of Michigan Press.
- Bauer, L.S., J.J. Duan, and J.R. Gould. 2014. Emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae.) Pp. 189–209 in *The Use of Classical Biological Control to Preserve Forests in North America*, R. van Driesche and R. Reardon, eds. Morgantown WV: U.S. Forest Service.
- Bentz, B., J. Logan, J. MacMahon, C.D. Allen, M. Ayres, E. Berg, A. Carroll, M. Hansen, J. Hicke, L. Joyce, W. Macfarlane, S. Munson, J. Negrón, T. Paine, J. Powell, K. Raffa, J. Régnière, M. Reid, B. Romme, S.J. Seybold, D. Six, D. Tomback, J. Vandygriff, T. Veblen, M. White, J. Witcosky, and D. Wood. 2009. *Bark Beetle Outbreaks in Western North America: Causes and Consequences*. Salt Lake City: University of Utah Press.
- Bentz, B.J., J. Régnière, C.J. Fettig, E.M. Hansen, J.L. Hayes, J.A. Hicke, R.G. Kelsey, J.F. Negrón, and S.J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *BioScience* 60(8):602–613.
- Berg, E.E., J.D. Henry, C.L. Fastie, A.D. De Volder, and S.M. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management* 227(3):219–232.
- Bergot, M., E. Cloppet, V. Péronaud, M. Déqué, B. Marçais, and M. Desprez-Loustau. 2004. Simulation of potential range expansion of oak disease caused by *Phytophthora cinnamomi* under climate change. *Global Change Biology* 10(9):1539–1552.
- Boyd, I.L., P.H. Freer-Smith, C.A. Gilligan, and H.C.J. Godfray. 2013. The consequence of tree pests and diseases for ecosystem services. *Science* 342:1235773.
- DeRose, R.J., and J.N. Long. 2014. Resistance and resilience: A conceptual framework for silviculture. *Forest Science* 60(6):1205–1212.
- Dukes, J.S., J. Pontius, D. Orwig, J.R. Garnas, V.L. Rodgers, N. Brazee, B. Cooke, K.A. Theoharides, E.E. Stange, R. Harrington, J. Ehrenfeld, J. Gurevitch, M. Lerda, K. Stinson, R. Wick, and M. Ayres. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Canadian Journal of Forest Research* 39(2):231–248.
- Early, R., B.A. Bradley, J.S. Dukes, J.J. Lawler, J.D. Olden, D.M. Blumenthal, P. Gonzalez, E.D. Grosholz, I. Ibañez, L.P. Miller, C.J.B. Sorte, and A.J. Tatem. 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications* 7:12485.
- Ellison, A.M., M.S. Bank, B.D. Clinton, E.A. Colburn, K. Elliott, C.R. Ford, D.R. Foster, B.D. Kloeppel, J.D. Knoepp, G.M. Lovett, J. Mohan, D.A. Orwig, N.L. Rodenhouse, W.V. Sobczak, K.A. Stinson, J.K. Stone, C.M. Swan, J. Thompson, B. Von Holle, and J.R. Webster. 2005a. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3(9):479–486.
- Ellison, A.M., J. Chen, D. Díaz, C. Kammerer-Burnham, and M. Lau. 2005b. Changes in ant community structure and composition associated with hemlock decline in New England. Pp. 280–289 in *Proceedings of the 3rd Symposium on Hemlock Woolly Adelgid in the Eastern United States*, B. Onken and R. Reardon, compilers. Morgantown, WV: U.S. Forest Service.
- Fissore, C., J.P. McFadden, K.C. Nelson, E.B. Peters, S.E. Hobbie, J.Y. King, L.A. Baker, and I. Jakobsdottir. 2012. Potential impacts of emerald ash borer invasion on biogeochemical and water cycling in residential landscapes across a metropolitan region. *Urban Ecosystems* 15(4):1015–1030.
- Ford, C.R., K.J. Elliott, B.D. Clinton, B.D. Kloeppel, and J.M. Vose. 2012. Forest dynamics following eastern hemlock mortality in the southern Appalachians. *Oikos* 121(4):523–536.
- Hauer, R.J., and W.D. Peterson. 2017. Effects of emerald ash borer on municipal forestry budgets. *Landscape and Urban Planning* 157:98–105.
- Jactel, H., M. Branco, P. Duncker, B. Gardiner, W. Grodzki, B. Langstrom, F. Moreira, S. Netherer, B. Nicoll, C. Orazio, D. Piou, M.-J. Schelhaas, and K. Tojic. 2012. A multicriteria risk analysis to evaluate impacts of forest management alternatives on forest health in Europe. *Ecology and Society* 17(4):52.
- Kautz, M., A.J.H. Meddens, R.J. Hall, and A. Arneeth. 2017. Biotic disturbances in Northern Hemisphere forests—a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. *Global Ecology and Biogeography* 26(5):533–552.

- Kovacs, K.F., R.G. Haight, D.G. McCullough, R.J. Mercader, N.W. Siegert, and A.M. Liebhold. 2010. Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. *Ecological Economics* 69(3):569–578.
- Krist, F.J., J.R. Ellenwood, M.E. Woods, A.J. McMahan, J.P. Cowardin, D.E. Ryerson, F.J. Sapio, M.O. Zweifler, and S.A. Romero. 2014. 2013–2027 National Insect and Disease Forest Risk Assessment. Fort Collins, CO: U.S. Forest Service.
- Lewis, K.J., and B.S. Lindgren. 2000. A conceptual model of biotic disturbance ecology in the central interior of B.C.: How forest management can turn Dr. Jekyll into Mr. Hyde. *Forestry Chronicle* 76(3):433–443.
- Liebhold, A.M., E.G. Brockhoff, S. Kalisz, M.A. Nuñez, D.A. Wardle, and M.J. Wingfield. 2017. Biological invasions in forest ecosystems. *Biological Invasions* 19(11):3437–3458.
- Lovett, G. M., M. Weiss, A. M. Liebhold, T. P. Holmes, B. Leung, K. F. Lambert, D. A. Orwig, F. T. Campbell, J. Rosenthal, D. G. McCullough, R. Wildova, M. P. Ayres, C. D. Canham, D. R. Foster, S. L. LaDeau, and T. Weldy. 2016. Nonnative forest insects and pathogens in the United States: Impacts and policy options. *Ecological Applications* 26:1437–1455.
- Morin, R.S., and A.M. Liebhold. 2015. Invasions by two non-native insects alter regional forest species composition and successional trajectories. *Forest Ecology and Management* 341:67–74.
- Perry, D.A. 1994. *Forest Ecosystems*. Baltimore: John Hopkins University Press.
- Peter, G.F. 2018. Breeding and engineering trees to accumulate high levels of terpene metabolites for plant defense and renewable chemicals. *Frontiers in Plant Science* online.
- Poland, T.M., and D.G. McCullough. 2006. Emerald ash borer: Invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry* 104(3):118–124.
- Raffa, K.F., E.N. Powell, and P.A. Townsend. 2013. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proceedings of the National Academy of Sciences of the United States of America* 110(6):2193–2198.
- Sambaraju, K.R., A.L. Carroll, J. Zhu, K. Stahl, R.D. Moore, and B.H. Aukema. 2012. Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. *Ecography* 35(3):211–223.
- Sharov, A.A., D. Leonard, A.M. Liebhold, E.A. Roberts, and W. Dickerson. 2002. "Slow the spread": A national program to contain the gypsy moth. *Journal of Forestry* 100(5):30–36.
- Weed, A.S., M.P. Ayres, and J.A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs* 83(4):441–470.
- Woodcock, P., J.E. Cottrell, R.J.A. Buggs, and C.P. Quine. 2017. Mitigating pest and pathogen impacts using resistant trees: A framework and overview to inform development and deployment in Europe and North America. *Forestry* 91(1):1–16.

Forest Health

This chapter contains the committee’s definition of forest health, which includes ecological, economic, and sociocultural factors. It summarizes the threats facing North American forests from insect pests and pathogens and introduces, as examples, the cases of four tree species affected by one or more of these pressures. These case study species are referenced throughout this report. This chapter concludes by describing the effects these threats have on forest health and ecosystem services.

DEFINING FOREST HEALTH

The committee spent much of its early deliberations discussing the term *forest health*. It heard a number of presentations on the topic (see Meeting 2 in Appendix B) and consulted the scientific literature (e.g., Kolb et al., 1994; Helms, 1998; Raffa et al., 2009; USDA–FS, 2009; Trumbore et al., 2015). On the basis of its information-gathering efforts, the committee agreed on the definition of *forest health* for this analysis as:

A condition that sustains the structure, composition, processes, function, productivity, and resilience of forest ecosystems over time and space. An assessment of this condition is based on the current state of knowledge and can be influenced by human needs, cultural values, and land management objectives.

Forest structure is the horizontal and vertical distribution of plant material, including ground vegetation and dead or fallen woody material, shrubs, and understory, midstory, and overstory trees (Bennett, 2010). Structure also concerns the age distribution of the trees in the forest. Forest stands are considered even-aged if all of the trees are within the same age class. A forest with uneven-aged structure is a stand with three or more age classes (Bennett, 2010). In practice, size is often used as a proxy for age. Forest structure affects seedling growth, survival, and crown formation of trees as well as the formation of habitat niches (von Gadow et al., 2012).

Forest composition refers to the identity and frequency of plant species found in a stand or landscape, including grass, forbs, shrubs, and trees. In other words, it is the entire plant community of the forest (Moore, 2004). Forest composition, directly or indirectly, affects all other biota present.

Trees play an important role in ecological processes, that is, the cycling of water, nutrients, and energy through the ecosystem, as well as in the natural successional dynamics, that is, the changes in plant species composition and structure following a disturbance (Glitzenstein et al., 1986; Keeton and Franklin, 2005). Trees’ influence on plant species composition and structure affects in turn the other species present in the system.

Healthy forests support economic, ecological, and sociocultural functions. Economic functions relate to the quality and quantity of timber or other vegetation products and game extracted from a forest as well as revenues generated through recreational uses of the forest. Ecological functions include habitat for wildlife, maintenance of biodiversity, soil erosion control, climate regulation, flood control, and effective maintenance of water quality. Sociocultural functions concern aesthetic, spiritual, and cultural values (DeFries et al., 2005; Cooper et al., 2016).

Forest productivity refers to the net primary productivity of plants in the forest system (reflected by the difference between the carbon captured via photosynthesis and that lost via respiration) (Landsberg and Waring, 1997).

Resilience in a forest ecosystem describes its capacity to absorb a disturbance¹ without a significant long-term change to the forest community functions and processes that existed before the disturbance (Holling, 1973; Millar and Stephenson, 2015; Seidl et al., 2016). For this report, resilience is specifically defined as a forest's ability to maintain its structure, processes, and functions in the long term; however, the committee was mindful of other aspects of resilience in response to disturbance (e.g., resistance, absorption, reorganization, and transformation; Fisichelli et al., 2016). In particular, transformative resilience, that is, the capacity to change into a new system when disturbance makes the existing system untenable (Walker et al., 2004), could be of great relevance in the context of using biotechnology in forest ecosystems.

Like forests themselves, the assessment of whether a forest is healthy is not static. The assessment of the health of a forest will change not only with the evaluation of its structure, composition, processes, function, productivity, and resilience, but also with the state of knowledge about these aspects of forest health. Increasing numbers of studies are also demonstrating that climate change is also altering various aspects of forest health (Boisvenue and Running, 2006; Reyer et al., 2017; Paquette et al., 2018).

THE VALUE OF HEALTHY FORESTS

A healthy forest can be valued for the benefits it provides to humans and also for its own sake. An instrumental view of forest health takes it as a means to an end: the betterment of human welfare. In contrast, the intrinsic value of a forest does not depend on its contribution to human society (NRC, 2005). While the instrumental valuation of the forest ecosystem is framed in terms of the services it provides to humans, intrinsic value concerns the value a forest may have in itself, independent of its usefulness to human beings. Here, both perspectives on valuation are introduced.

Maintaining forest health is essential for the conservation and sustainable management of the many ecosystem services provided to humans by forests. Ecosystem services are the goods and services that are of value to people, provided wholly or in part by ecosystems (Olander et al., 2015). In 2005, the Millennium Ecosystem Assessment categorized these services as provisioning, regulating, supporting, and cultural (Shvidenko et al., 2005; see Box 2-1).

Many ecosystem services that are provisioning, regulating, or supporting are biologically mediated (Burkhard and Maes, 2017). Trees help form and retain soil, cycle nutrients, and store carbon (e.g., Seidl et al., 2016). They filter and regulate the flow of water, first by intercepting rainfall in the canopy. The reduced volume and speed of the rain allows more water to be absorbed into the ground and, combined with the roots' soil retention properties, controls flooding and reduces erosion (Ellison et al., 2017). Second, roots take up nutrients and pollutants in the subsurface water, preventing these elements from filtering into the groundwater supply. Trees improve air quality by intercepting pollutant particles (Nowak et al., 2014). Water vapor cools the surrounding environment when it evaporates from leaves. Trees buffer the landscape from the heat of the sun and the force of winds, and forests provide food and habitat for pollinators, fish, wildlife, and other organisms, as well as food, fuel, and products for humans.

¹Natural disturbance is part of the normal functioning of a forest. Forested systems undergo successional and cyclical changes in structure and composition, which help to maintain high levels of biodiversity (Perry, 1994; Barnes and Wagner, 2004). Healthy forests may withstand natural disturbances either by being able to maintain similar properties (i.e., showing resistance) or by being able to recover many of their original properties afterward (i.e., being resilient). Land management practices can influence forest function and productivity following disturbance (Millar and Stephenson, 2015).

BOX 2-1 Ecosystem Services

Ecosystem services are the benefits that society obtains from ecosystems. Forest ecosystem services are classified into four groups.

- *Provisioning services*: Goods or products obtained from ecosystems such as food and medicinals, fresh water, raw materials for building, clothing, energy, and ornamental and horticultural resources.
- *Regulating services*: Benefits obtained from an ecosystem's control of natural processes such as soil formation, stabilization and erosion, water seasonal-flow regulation and filtration/purification, flood control, air quality regulation, carbon sequestration and storage, climate regulation, pollination, insect pest and disease regulation, waste decomposition and detoxification, and natural hazard regulation.
- *Supporting services*: Natural processes necessary for the production of other ecosystem services. They include maintaining biogeochemical and nutrient cycles, soil formation, soil fertility, and primary production.
- *Cultural services*: Benefits humans obtain through spiritual enrichment, cognitive development, health improvement, recreation, education, and aesthetic experiences.

SOURCE: DeFries et al. 2005.

Cultural ecosystem services are diverse (Milcu et al., 2013). They vary according to the intended or desired use of an ecosystem, such as recreation or creation of traditional forest products. Additionally, forests provide substantial cultural heritage or identity and spiritual, educational, and aesthetic values (Cooper et al., 2016). The values at stake may vary by individual or group. For example, some people may value mountain bike trails through a forest, whereas others may value the same area for its wildlife viewing opportunities or for a spiritual connection felt to nature when in that space. People may also place *existence* or *nonuse* value on forests simply because they wish to preserve the ecosystem or species within it (NRC, 2005).

Alongside the services they provide to humans, ecosystems such as forests may also be thought to have *intrinsic* value, value for their own sake. Intrinsic value, however, can be understood in different ways. *Subjective* intrinsic value arises from human evaluative attitudes. In the context of forests, for instance, people might intrinsically value forest ecosystems or wild animals or the perceived state of wildness itself. *Objective* intrinsic value describes value that is believed to exist on the basis of certain properties or features, independent of anyone's evaluative attitudes (Sandler, 2012, 2018). If someone argues that human lives are valuable on the basis of certain properties humans have, whether or not anyone *actually* values human lives, then they are defending the objective intrinsic value of human life. If someone argues that a forest ecosystem is objectively intrinsically valuable, they are maintaining that it has intrinsic value whether or not any human actually values it. Although the existence of objective intrinsic value is disputed on the ground that values must be created by valuers, the existence of objective intrinsic value in species, ecosystems, individual organisms, or all three has often been assumed or defended in conservation and environmental ethics (e.g., Soulé, 1985; Taylor, 1986; Rolston, 1988).

The relationship between intrinsic value and existence value is complex. Because existence value is based on human preference, it is clearly distinct from objective intrinsic value. Existence value and subjective intrinsic value, however, are much closer in meaning, and some definitions take existence value to be synonymous with subjective intrinsic value (e.g., Aldred, 1994). However, Davidson (2013:175) interprets existence value "as the (willingness to pay for the) *benefits* one derives from something's mere existence, although one has no current or future plans for its active use." Existence value, on this account, entails some kind of benefit or satisfaction to the valuer. Intrinsic value, on the other hand, does not imply any benefit to the valuer; rather, the existence of something with intrinsic value "exerts a moral duty on us to take it

into account.” Therefore, Davidson suggests something could have intrinsic value without existence value; for example, a rat in a kitchen has intrinsic value, in that the human in the kitchen has a duty not to harm it, but presumably that person would prefer for the rat not to exist at all. Given this understanding of intrinsic value, Davidson argues that intrinsic value, though not existence value, falls outside the scope of ecosystem services because it is not in any sense about nature’s services to humans.

In this report, the committee adopts ecosystem services as the basis for assessment of the instrumental impacts of introducing a biotech tree to counter a threat to forest health. Chapter 5 presents a specific framework for defining ecosystem services in impact assessment that is compatible with regulatory decision making (discussed in Chapter 6). The impact assessment considers the potential benefits, risks, and trade-offs of the introduction of a biotech tree by evaluating expected changes in forest ecosystem services. However, the committee also believes that consideration of the intrinsic values of a healthy forest could usefully broaden the scope of public deliberations about the use of biotechnology (discussed in Chapter 7). Chapter 4 considers some of these values and the ways in which they may be affected by the introduction of a biotech tree to a forest ecosystem.

A healthy forest—that is, one in a condition that sustains the components of an ecosystem over time and space—is more likely to sustain ecosystem services of value to individuals and society. When assessing the impact of a threat (such as an invasive insect) on forest health, evaluating the effect of that threat on the biologically mediated processes and the cultural and aesthetic values of the forest ecosystem provides the basis for assessing how the provision of ecosystem services may change. When adverse effects are experienced or anticipated, alternative means of returning the forest ecosystem to health are considered, including the introduction of a biotech tree that can resist the threat. The remainder of this chapter reviews the scope of the threat from insect pests and pathogens facing North American forests and the implications of that threat for the forest ecosystem and the ecosystem services it provides.

THREATS TO FOREST HEALTH FROM INSECT PESTS AND PATHOGENS

Despite being part of the forest natural disturbance regime, outbreaks of insects and pathogens have dramatically increased in number and impact since the mid-19th century (Aukema et al., 2010; Boyd et al., 2013). The most recent national insect and disease risk assessment, conducted in 2012 by the Forest Service of the U.S. Department of Agriculture (USDA), estimated that 32.9 million hectares (81.3 million acres)—that is, almost 7 percent of all forested² or treed³ land in the United States—were at risk of losing at least 25 percent of tree vegetation between 2013 and 2027 due to insects and diseases (see Figure 2-1; Krist et al., 2014). That assessment placed 9.4 million more hectares (23.3 million acres) at risk than was estimated in 2006 (Krist et al., 2014).

Most of these outbreaks have been caused by introduced insects and pathogens or by native species within their natural range as well as those expanding their geographic ranges due to climate change (Liebhold et al., 1995; Lovett et al., 2006; Sambaraju et al., 2012; Weed et al., 2013). Climate change is further compounding the impact of insects and pathogens by increasing abiotic stresses on trees, which may result in reduced defenses and increased susceptibility (Breshears et al., 2005; Berg et al., 2006). As a result, the impacts of insects and pathogens are among the greatest threats to forest ecosystems in North America (Moser et al., 2009; Krist et al., 2014; Lovett et al., 2016).

As the frequency of insect and pathogen outbreaks increases, forest resilience and the ecosystem services associated with forests are threatened (Millar and Stephenson, 2015; Seidl et al., 2016). The next section describes general threats posed by insects and pathogens and their interaction with climate change.

²Forested land contains at least 10 percent tree canopy cover.

³Treed land is an area with measurable tree presence, including urban areas and land in the Great Plains with trees that does not meet the definition of forested land.

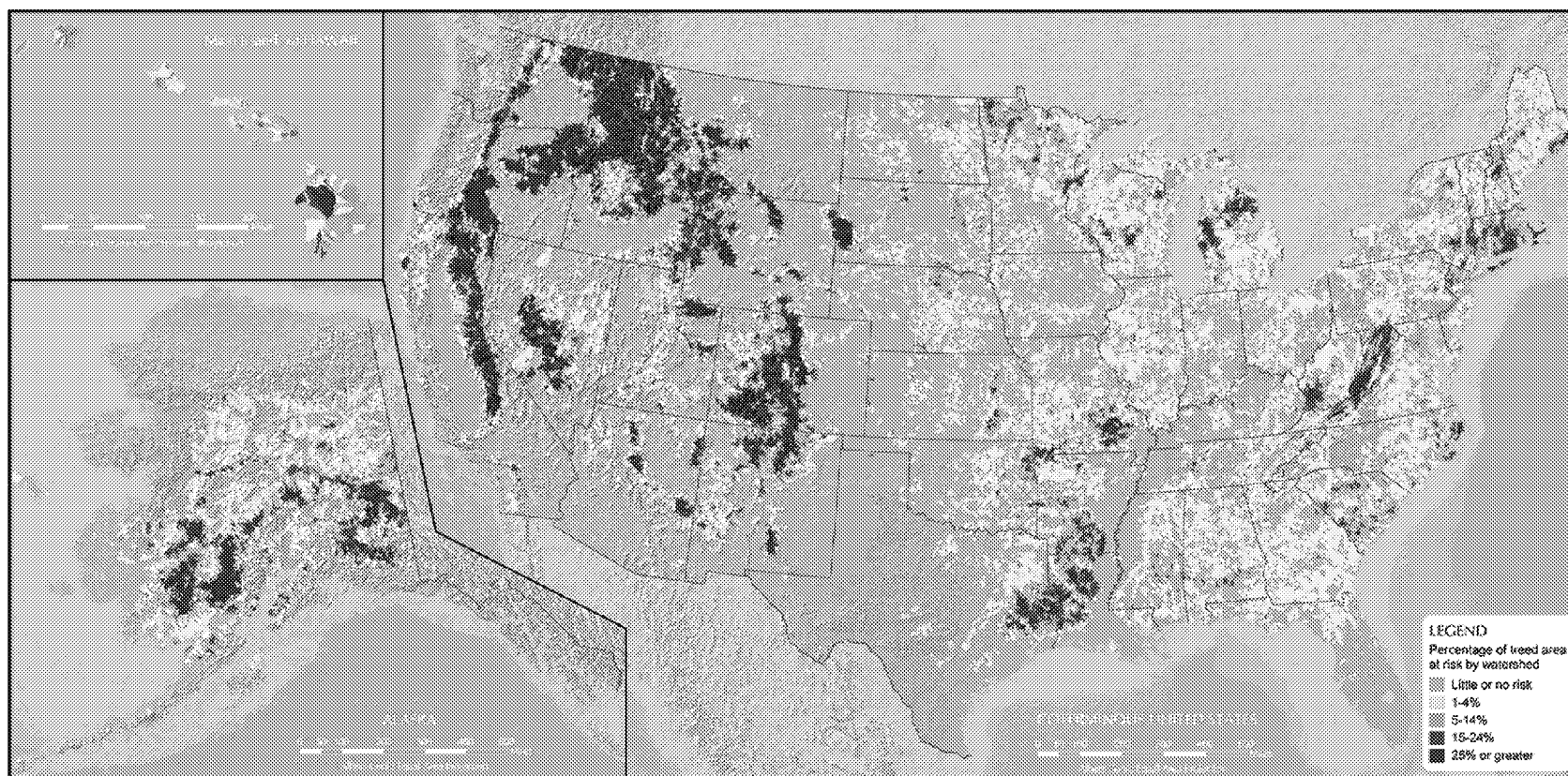


FIGURE 2-1 Risk assessment from insect pests and diseases in U.S. forests by subwatershed, 2013–2027. NOTE: Hectares at risk total 32.9 million.
SOURCE: Krist et al. 2014.

Introduced Insect Pests and Pathogens

Since the 1600s, around 450 species of insects and at least 16 species of pathogens have been introduced and become established in continental U.S. forests. Of those, 14 percent of the insects (62 species) and all of the pathogens have been classified as high-impact species (Aukema et al., 2010); that is, they cause some combination of tree mortality, canopy thinning, growth loss, defoliation, and decreased reproduction or regeneration. At least 2.5 introduced, established insect species have been detected each year since 1860 (Aukema et al., 2010). Given their cryptic nature and difficulties in early detection, there is little information on the rate of pathogen introduction.

Increases in human mobility and trade are the major pathways of introductions (Pyšek et al., 2010; Brockerhoff et al., 2014; Early et al., 2016). Pathogens and insect defoliators have generally been introduced with live plants (Liebhold et al., 2012). The introduction of insect borers, the most damaging group (see Box 2-2), is usually associated with wood packaging material (Aukema et al., 2010, 2011). The number of introduced borer species (including bark and ambrosia beetles) has dramatically increased since the 1990s, averaging 1.6 new introductions per year, reflecting the increased use of wood packaging materials and the growth in global trade (see Figure 2-2; Haack, 2006; Aukema et al., 2010). These introductions continue despite proactive requirements for treatment of wood pallets and shipping containers (Haack et al., 2014).

Some of these introductions have had devastating consequences in North American forests; impacts have ranged from temporary declines in population productivity to the functional extirpation of an entire species (see case study of the American chestnut, below). In many instances, the introduced insect pests and pathogens lack natural competitors, predators, parasites, or pathogens to regulate their populations (i.e., enemy release; Keane and Crawley, 2002), giving them a temporary fitness advantage that could contribute to their virulence (Hajek et al., 2016). The damage these species cause can be linked to a lack of resistance in the host tree (Herms and McCullough, 2014). Table 2-1 summarizes many of the nonnative pests threatening North American tree species.

BOX 2-2 Effects of Insect Pests and Pathogens

Among insect pests, phloem and wood-boring species cause the most damage to forest trees, followed by sap feeders and then by foliage feeders (Aukema et al., 2011). Borers are species of beetles, wasps, and moths that can be extremely destructive in their larval stage. They damage the tree's vascular system, which often results in the death of the tree, and they produce tunnels that reduce the structural soundness of the wood and allow rotting fungi to enter. The invasive emerald ash borer (*Agrilus planipennis*) is an example of a wood borer and the native mountain pine beetle (*Dendroctonus ponderosae*) is an example of a phloem-boring bark beetle.

Sap feeders (adelgids, scales, and aphids) pierce leaves and stems to suck out plant nutrients. Infestations by native sap feeders rarely lead to death, although they can reduce growth, reproduction, and productivity of plants (Zvereva et al., 2010). In contrast, introduced sap feeders such as the balsam woolly adelgid (*Adelges piceae*) and the hemlock woolly adelgid (*Adelges tsugae*) kill native trees in high numbers. Insect herbivory of leaf tissue by foliage feeders can reduce growth and productivity and during outbreaks can lead to the mortality of thousands of trees such as what occurs periodically with spruce budworm (Lepidoptera: Tortricidae) (Ludwig et al., 1978).

Among tree pathogens, fungi and oomycetes (which cause seedling blights, damping-off, root rots, and foliar blights) have the most devastating effects on forest species, often resulting in tree mortality and, in extreme cases, in the local extirpation of the host species. They can damage and reduce leaf area, harm roots, and cause vascular wilts and cankers that reduce the flow of water (Latijnhouwers et al., 2003). Chestnut blight, for example, is caused by the fungus *Cryphonectria parasitica*; sudden oak death results from infection by the oomycete *Phytophthora ramorum*.

Additionally, insects are often the vectors of pathogens that are the actual agent of mortality. For example, the boring redbay ambrosia beetle (*Xyleborus glabratus*) introduces a fungus (*Raffaelea lauricola*) that causes laurel wilt, a deadly disease of redbay (*Persea borbonia*) and other tree species in the laurel family (Lauraceae) (Kendra et al., 2013). The sap-sucking beech scale (*Cryptococcus fagisuga*) transmits the fungi that cause beech bark disease (Castlebury et al., 2006).

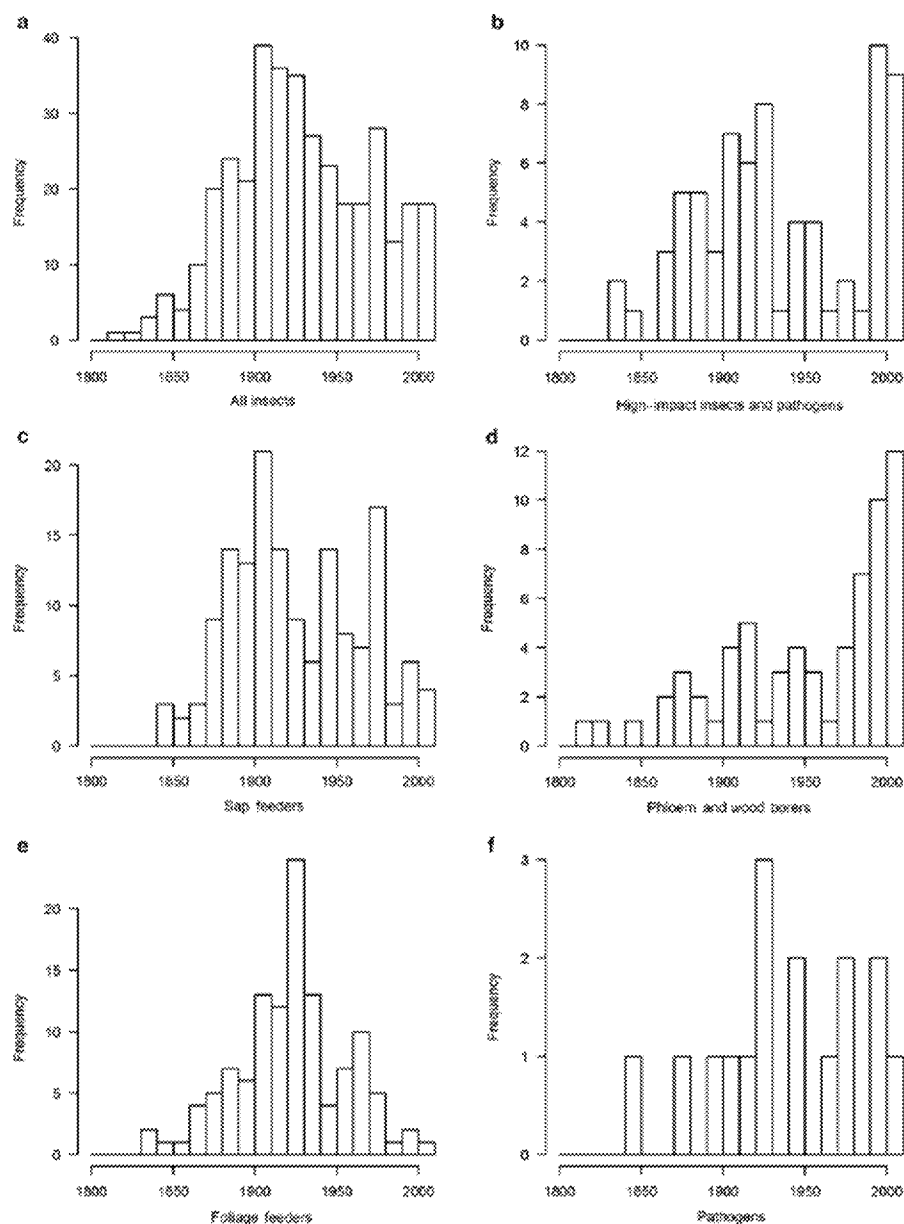


FIGURE 2-2 Frequency of detection of introduced insects and diseases in continental United States through 2006. (a) All introduced forest insects; (b) high-impact insects and pathogens (those that cause some combination of tree mortality, canopy thinning, growth loss, defoliation, and decreased reproduction or regeneration); (c) sap-feeding insects; (d) phloem and wood-boring insects; (e) foliage feeders; and (f) pathogens. SOURCE: Aukema et al., 2010.

The majority of introduced insect pests and pathogens are found in the northeastern United States (Liebhold et al., 2013; see Figure 2-3). This geographic pattern likely reflects the number of introductions, the historically high propagule pressure, and the impact of anthropogenic disturbance on the ability of the pests to invade in this region (Liebhold et al., 2013). This distribution is also correlated with the diversity of tree species, which is higher in the eastern half of the country (Liebhold et al., 2013). Once established, the average radial rate of spread—5.2 km per year—seems to be similar for all groups of insect pests and pathogens (Liebhold et al., 2013).

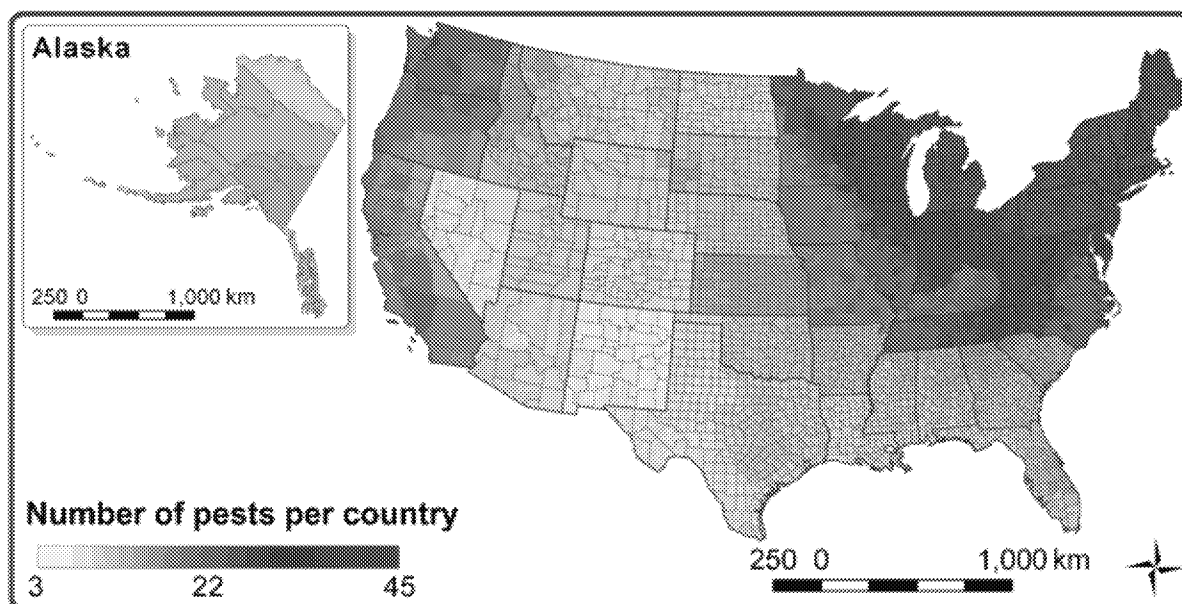


FIGURE 2-3 Number of high-impact invasive insect pests and pathogens in forests (per county) in the continental United States and Alaska. NOTE: High-impact species are those that cause some combination of tree mortality, canopy thinning, growth loss, defoliation, and decreased reproduction or regeneration. SOURCE: Liebhold et al., 2013.

Insect Pests and Pathogens Under Climate Change

Climate change is opening new opportunities for colonization by both native and introduced insect species (Harvell et al., 2002; Logan et al., 2003). Forecasted temperatures for the mid-21st century indicate decreases in the length of the cold season and the incidence of extreme cold spells (IPCC, 2013). Cold winter temperatures, cold snaps, and short growing seasons have kept many insect pest species in the United States from moving into higher elevations and more northern latitudes (Carroll et al., 2004; Esper et al., 2007; Dukes et al., 2009). However, with warmer conditions, many insects are colonizing regions that previously had been unsuitable (Williams and Liebhold, 1997; Battisti et al., 2005). In addition, changes in climate are affecting the frequency and magnitude of outbreaks of both native and introduced pests. Outbreaks are predicted to increase in frequency and magnitude in the future. In areas where cold has previously limited establishment, warmer temperatures will likely allow an increase in development and reproductive rates and survival of many insects and pathogens (Ayres and Lombardero, 2000; Bale et al., 2002). An example is the native mountain pine beetle (*Dendroctonus ponderosae*) outbreak in North America between 1990 and 2010, which killed millions of hectares of pines and has been estimated to be an order of magnitude larger than any previously recorded event (Meddens et al., 2012; Raffa et al., 2013). This outbreak was associated with a reduction in cold snaps (i.e., periods of four consecutive days with average temperature below -20°C) (Sambaraju et al., 2012) and overall warmer summer and winter temperatures. Warmer temperatures have also allowed an expansion of the territory of the mountain pine beetle hundreds of kilometers farther north in British Columbia and movement across Alberta into jack pine forests (*Pinus banksiana*), where it threatens the boreal forest as an invader. Likewise, southern pine beetle (*Dendroctonus frontalis*) is moving northward into new forests on the eastern coast of the United States. In Alaska, Canada, and Colorado, outbreaks of spruce beetle (*Dendroctonus rufipennis*) have increased with warmer weather and drier summers (Berg et al., 2006), and the beetle's spread has been predicted to increase as warmer conditions facilitate faster insect development (Bentz et al., 2010; see Figure 2-4).

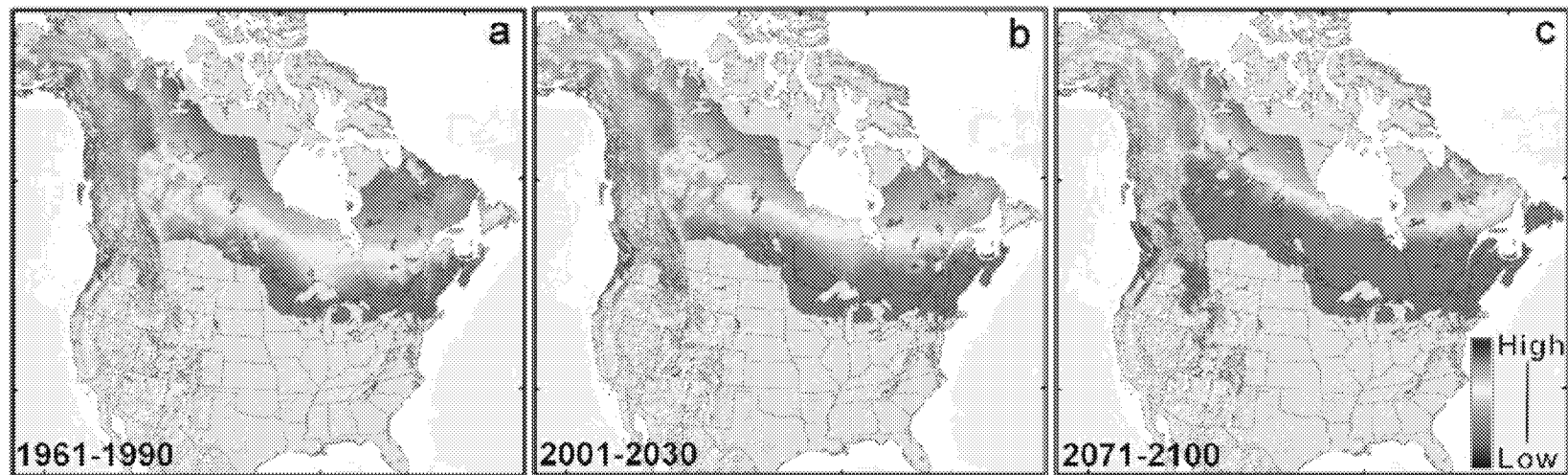


FIGURE 2-4 Estimated probability of spruce beetle developing in a single year in North American spruce forests: (a) 1961–1990, (b) 2001–2030, and (c) 2071–2100. SOURCE: Bentz et al., 2010.

Changes in temperature and precipitation associated with climate change may become the most influential driver of pathogen outbreaks, because these changes could simultaneously affect host susceptibility and pathogen growth, reproduction, and infection (Sturrock et al., 2012). Forecasts of future climate indicate likely changes in pathogen overwintering survival, changes in host susceptibility to pathogen attack due to other stressors (e.g., drought conditions, ozone, or damage from storms), or changes in life cycles of associated species such as insects that disperse pathogens (Dukes et al., 2009; Weed et al., 2013). However, the outcome of these changes—higher or lower virulence—will likely be site specific (Sturrock et al., 2012). For example, *Phytophthora ramorum*, an introduced oomycete that causes sudden oak death, may experience a decrease in favorable environmental conditions in the eastern United States, but an increase in favorable sites in the western United States (Venette and Cohen, 2006; Venette, 2009) and Europe in response to climate change (Bergot et al., 2004).

Given that some pathogen species rely on insects for their dispersal (Wingfield et al., 2016), effects of climate change on the insect populations would likely cause changes in pathogen dynamics. For example, the two fungi that cause beech bark disease (*Neonectria farinata* and *N. ditissima*) are spread by a scale insect, *Cryptococcus fagisuga*. The extent of the infestation had been restricted by cold winter temperatures, but with the onset of mild winters and dry autumns associated with climate change, both the scale and the fungi will likely move to northern latitudes and affect beech trees that had previously been shielded from the pathogen (Houston and Valentine, 1988; Stephanson and Coe, 2017).

EFFECTS OF INSECT PESTS AND PATHOGENS ON TREES AND ECOSYSTEM SERVICES

Adverse effects on forest health caused by increases in the frequency and magnitude of insect and pathogen outbreaks are already being observed and are likely to continue. This section reviews the effects on some specific tree species and genera; the feasibility of using biotechnology to address threats to these species is discussed in subsequent chapters. This section also examines more broadly the effects of insect pests and pathogens on forest health and ecosystem services.

Case Study Trees

A variety of introduced insect pests and pathogens (many included in Table 2-1) and the exacerbated pressure of some native insects and diseases facilitated by climate change threaten the long-term survival of many forest tree species native to North America. Rather than elucidating all threats, the committee decided to focus on four cases chosen by consensus and based on the following criteria:

- The severity of the threat.
- The causative agent(s) (insect, pathogen, or complex systems involving insect vectors or obligate pathogens with alternate hosts).
- The origin of the insect or pathogen (native or nonnative).
- The impact of climate instability and fire on the severity and extent of the disease or infestation.
- The ecological, economic, and cultural values of the host tree species.
- The use or potential use of the host tree species for plantation forestry.
- The efficacy or feasibility of traditional strategies to protect forest health (biological control, pesticide use, containment strategies, and selective tree breeding).
- The efficacy of gene insertion or gene-editing strategies if already in place.
- The feasibility of gene insertion or gene-editing strategies if not yet attempted or tested.
- Geographical distribution and phylogenetic position of the host species.

TABLE 2-1 Eighteen Nonnative Forest Insects and Pathogens in North America with Current or Potential Future High Impacts

Common Name	Scientific Name	Pathway	Hosts	Impacts	Geographic Region at Risk
<i>Established Species with High Impact</i>					
Chestnut blight	<i>Cryphonectria parasitica</i> (Murrill) Barr.	Live plants	American chestnut, chinquapin	Virtually eliminated mature chestnuts	Eastern deciduous forest
White pine blister rust	<i>Cronartium ribicola</i> J. C. Fisch	Live plants	Five-needle pines (section <i>Quinquefolia</i> in genus <i>Pinus</i>)	High mortality of susceptible trees in several western pine species	Continent-wide; greatest impacts in West
Phytophthora dieback	<i>Phytophthora cinnamomi</i> Rands	Unknown	Many hosts including American chestnut, white oak, shortleaf pine, and Fraser fir, fruit trees	High mortality of susceptible trees	Continent-wide
Port-Orford-cedar root disease	<i>Phytophthora lateralis</i> Tucker & Milbrath	Probably live plants	Port-Orford-cedar	High mortality of trees, especially in riparian parts of its range	Klamath Mountains, California and Oregon
Beech bark disease (scale insect + fungus)	<i>Cryptococcus fagisuga</i> Lindinger + <i>Nectria coccinea</i> var. <i>faginata</i> (Pers.) Fr.	Live plants	American beech	Severely reduces mature beech; often replaced by dense thickets of root sprouts	Deciduous forests of East and Midwest
European gypsy moth	<i>Lymantria dispar dispar</i> L.	Escaped from deliberate introduction	Many hosts includes oaks, aspen, willow, and birch	Periodic outbreaks cause defoliations and can sometimes kill hosts	Deciduous forests of East and Midwest
Hemlock woolly adelgid	<i>Adelges tsugae</i> Ammand	Live plants	Eastern and Carolina hemlock	High mortality in most affected stands	Appalachians, Northeast, and upper Midwest
Sudden oak death	<i>Phytophthora ramorum</i> S. Werres, A.W.A.M. de Cock	Live plants	>100 spp., especially tanoak and several western oak species; some eastern oaks vulnerable	High mortality in some vulnerable hosts (particularly tanoak); other hosts show minor impacts	Coastal California and Oregon; could potentially spread to eastern forests
Redbay ambrosia beetle + fungus (laurel wilt disease)	<i>Xyleborus glabratus</i> Eichhoff + <i>Raffaelea lauricola</i> Harrington and Fraedrich	Wood packaging	Numerous probable hosts including redbay and pondberry & pondspice shrubs	Predicted >90% reduction in redbay basal area within 15 yr (25 yr after first detected)	Eastern deciduous forests; greatest impacts in southeastern coastal plain
Emerald ash borer	<i>Agrilus planipennis</i> Fairmaire	Wood packaging	All North American ash species	Most ash trees succumb; some species of ash appear to have limited resistance	Eastern deciduous forest; riparian areas in Great Plains and West, landscape plantings continent-wide
Dutch elm disease	<i>Ophiostoma ulmi</i> (Buisman) Nannf. & <i>O. novo-ulmi</i> Brasier; vectored by several insects including <i>Scolytus multistriatus</i> and <i>S. schevyrewi</i>	Wood products	American elm; other native elms, e.g., red or slippery elm, are more resistant	Severe impacts in urban areas; elms remain, although reduced in number and size, in riparian woodlands	Continent-wide

(Continued)

TABLE 2-1 Continued

Common Name	Scientific Name	Pathway	Hosts	Impacts	Geographic Region at Risk
Butternut canker	<i>Sirococcus clavignenti-juglandacearum</i> N. B. Niar, Kostichka & Kuntz	Unknown	Butternut (white walnut)	Severe mortality of butternut; over 80% mortality of butternut in the South	Deciduous forests of Northeast and Midwest
Balsam woolly adelgid	<i>Adelges piceae</i> Ratzeburg	Live plants	Most true fir species (<i>Abies</i>) in North America	Widespread impacts on firs; severe mortality of Fraser fir on southern Appalachian mountaintops and Christmas tree farms	Northeast; southern Appalachians; Northwest
<i>Established, Potential for Significant Effects in the Future</i>					
Asian longhorned beetle	<i>Anoplophora glabripennis</i> Motschulsky	Wood packaging	Woody vegetation in 15 families, especially maples, elms, and willows	Severe impacts possible in both urban and forest landscapes; eradication being attempted	Continent-wide deciduous forests
Winter moth	<i>Operophtera brumata</i> L.	Unknown	Many species including oaks, maples, cherries	Severe impacts on hosts in southeastern New England	Eastern deciduous forest
Polyphagous shot hole borer and fusarium fungus	<i>Euwallacea</i> (sp. unknown) + <i>Fusarium euwallacea</i>	Unknown	>200 species attacked by insect; >100 support the fungus; hosts killed include box elder, bigleaf maple, coast live oak	High mortality levels in vulnerable hosts	Southern California hardwood forests, riparian and urban; potentially in Southeast
European woodwasp	<i>Sirex noctilio</i>	Probably wood packaging	Many pine species	Most important killer of pines in Southern Hemisphere; modest impacts so far in United States	All ecosystems with hard pines; Southeast, Great Lakes states, western United States
<i>Not Yet Established</i>					
Asian gypsy moth & hybrids	<i>Lymantria dispar asiatica</i> Vinuskovkij	Ship super-structures	>600 species, including common deciduous and coniferous trees	Could have more severe impacts than European gypsy moth since it has wider host range and females fly	Continent-wide

SOURCE: Adapted from Lovett et al., 2016.

The four selected case studies—American chestnut (*Castanea dentata*), whitebark pine (*Pinus albicaulis*), ash (*Fraxinus* spp.), and poplar (*Populus* spp.)—represent a wide range of forest health problems with different combinations of characteristics in terms of the above criteria (Table 2-2). In two cases, the committee chose specific host trees that face more than one pest pressure (American chestnut and whitebark pine). In the other two cases (ash and poplar), the committee examined the implications of a specific pest for a genus of trees. The native ranges of the major host tree species vary considerably in extent but together cover much of the United States (see Figure 2-5). Forest ecosystems, rural and urban, have all experienced negative ecological and economic impacts from tree mortality caused by the insects and pathogens examined in these studies. All of the species have clear ecological and cultural value, and all but whitebark pine have economic value. Critical for this study, the species vary in development and feasibility of a biotech solution to reduce vulnerability to the insect pest or pathogen involved. The case studies are introduced here and referenced throughout the rest of the report.

TABLE 2-2 List of Variables Considered by the Committee When Selecting Case Studies

Variable	American Chestnut (<i>Castanea dentata</i>)	Whitebark Pine (<i>Pinus albicaulis</i>)	Ash (<i>Fraxinus</i> spp.)	Cottonwood (<i>Populus trichocarpa</i> , <i>P. balsamifera</i>)
Geographic distribution	Eastern North America	Western North American mountains	16 species widely distributed across North America	Northern and western North America
Causative agent (origin)	Pathogen: chestnut blight (<i>Cryphonectria parasitica</i>) (nonnative)	Pathogen: <i>Cronartium ribicola</i> (nonnative) Insect pest: mountain pine beetle (<i>Dendroctonus ponderosae</i>) (native)	Insect pest: emerald ash borer (<i>Agrilus planipennis</i>) (nonnative)	Pathogen: <i>Sphaerulina musiva</i> (native to eastern species of poplar but not to northern and western species)
Other stressors	Pathogen: <i>Phytophthora cinnamomi</i> (nonnative) Insect pest: <i>Dryocosmus kuriphilus</i> (nonnative)	Climate change (drought), changes in fire regime	Land conversion	Land conversion, flood control
Urgency	High	High	High	Low
Alternative insect/pathogen hosts	Yes	Yes	Yes	Yes
Major ecological role	Yes	Yes	Yes	Yes
Economical values	Timber, chestnuts	None	Landscaping, timber, woodworking products	Pulp production
Cultural/traditional values ^a	Yes	Yes	Yes	Yes
Plantation forestry	Maybe	No	No	Yes
Potentially effective nonbiotech approaches to mitigate forest health threats ^b	Hybridization (breeding) Hypovirulence	Reduced abundance of alternative hosts. Selective breeding for resistance	Biocontrol (parasitoids), pesticides. Selective breeding for resistance	Fungicide application Biocontrol (bacteria)
Biotechnological approaches in use as of 2018 ^c	Transgenesis	None	None	Transformable with <i>Agrobacterium</i>
Potential biotechnological approaches ^c	Well developed	Recalcitrant	In development	Well developed

^aSee discussion in section “Social and Ethical Considerations” in Chapter 4.

^bSee Boxes 3-1 and 3-2 in Chapter 3.

^cSee Box 3-4 in Chapter 3.

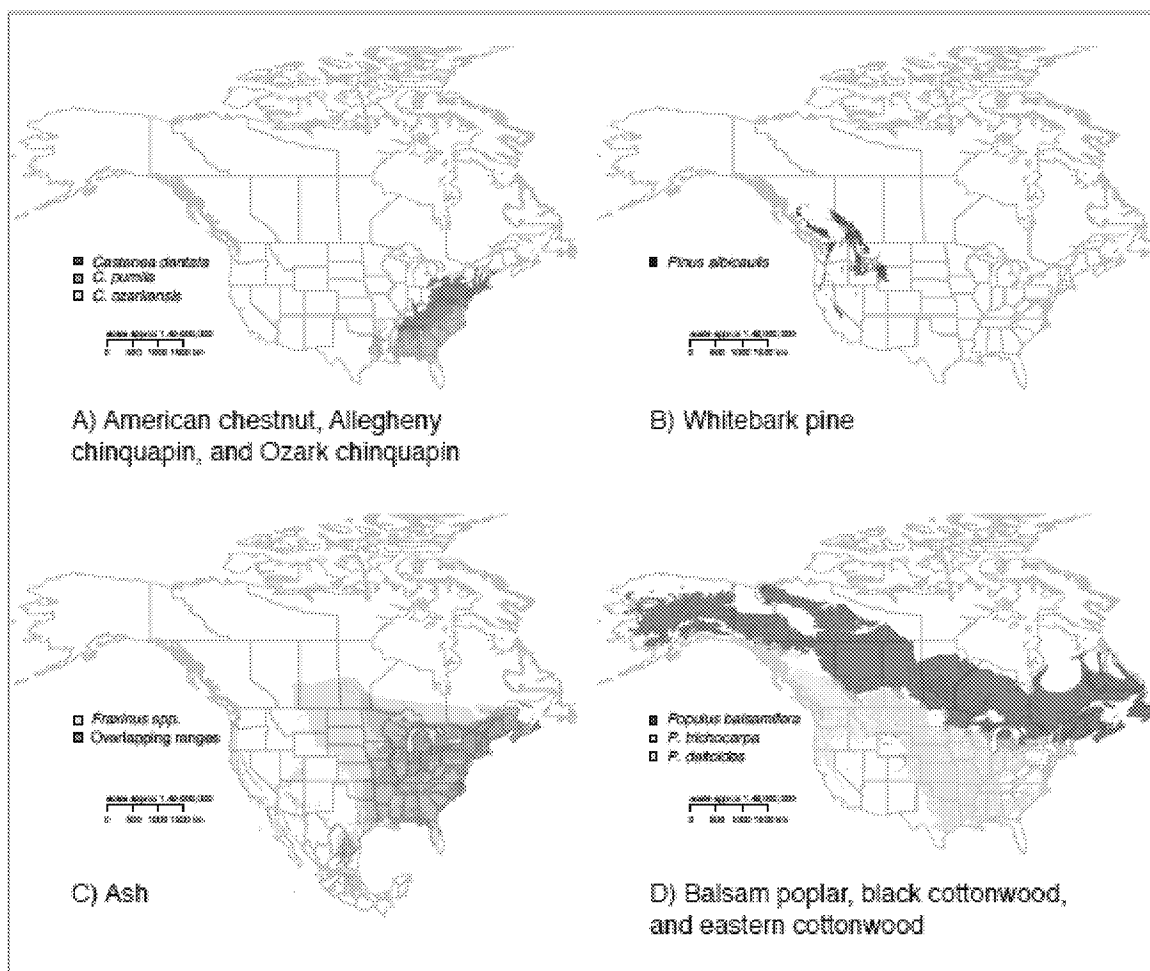


FIGURE 2-5 Geographical ranges of case study species: (a) American chestnut and relatives Allegheny chinquapin and Ozark chinquapin, (b) whitebark pine, (c) ash species, (D) balsam poplar (*Populus balsamifera*), black cottonwood (*P. trichocarpa*), and eastern cottonwood (*P. deltoides*). IMAGE CREDIT: V. Chhatre.

American Chestnut (*Castanea dentata*)

In the 19th century, the range of American chestnut extended from Maine to Mississippi along the Appalachian Mountains (see Figure 2-5; Little, 1977). American chestnuts were fast growing, and trees could reach 37 meters in height and 5 meters in diameter on favorable sites (Buttrick, 1925; Wang et al., 2013). The number of mature trees prior to the introduction of chestnut blight was estimated to be four billion (Detwiler, 1915), representing a major fraction of the forest biomass in many eastern forests (Braun, 1950). At some locations in the Appalachian Mountains, the American chestnut was considered to be a foundation species because of its strong influence on ecosystem structure and function (Youngs, 2000; Ellison et al., 2005a). In some regions, one in four trees in the canopy was reported to be an American chestnut (Johnson, 2013).

In 1904, American chestnuts at the Bronx Zoo in New York City died from infection by a fungal pathogen initially identified as *Diaporthe parasitica* but later renamed *Cryphonectria parasitica*. The pathogen was likely introduced on Japanese chestnuts imported to the United States as early as 1876 (Anagnostakis, 1987; Anagnostakis and Hillman, 1992).

The disease spread more or less unchecked, extending over the entire range of the American chestnut by the 1950s (see Figure 2-6). Traditional control measures, such as chemical treatments or clearing and burning, were ineffective (Stoddard and Moss, 1913). The pathogen maintained virulence over time, and almost all mature chestnuts were killed (Hepting, 1974; Russell, 1987).

The pathogen causing chestnut blight is necrotrophic, entering through small wounds in the outer bark, killing the living vascular cambium, and then developing cankers on the dead tissues. In susceptible trees, the fungus eventually girdles the branches and main stem, blocking the transfer of nutrients and resulting in tree death (Anagnostakis, 2000). In blight-tolerant Asian chestnut trees, lignified callus may surround the wound and restrict the growth of cankers; in susceptible trees, the fungus is able to overcome this resistance, leading to mortality.

In 2018, surviving chestnut trees existed mainly in shrubby growth forms that result from the formation of sprouts from the root collar. The sprouts grow for several years until they are again infected by *C. parasitica* and die back. Each cycle—resprout followed by fungus infection and dieback—weakens the tree until it eventually dies (Griffin, 2000). Sprouts rarely reach reproductive maturity and seeds are seldom produced (Paillet, 2002). Thus, the American chestnut persists mainly as a multistemmed shrub with only a few large chestnut trees remaining, often at the periphery of the tree’s range, presumably as “escapes” (i.e., trees that have not yet been exposed to the pathogen).

The loss of the American chestnut was devastating for rural communities that depended on the tree for food, livestock feed, and timber (Youngs, 2000; Freinkel, 2009). Equally devastating were the changes to the forest ecosystem due to the loss of a foundational species (Freinkel, 2009).

Other nonnative *Castanea* species have been planted in urban environments or as orchard trees for commercial production of chestnuts, but they do not fill the same ecological niche as the American chestnut. Chinese chestnut (*C. mollissima*) and Japanese chestnut (*C. crenata*) are typically small trees, lacking the fast growth and tall form of American chestnut. The European chestnut (*C. sativa*) has a growth and form somewhat similar to American chestnut as compared to the Asian species, but the European chestnut trees growing in North America are susceptible to the same diseases as the American chestnut and are not as frost tolerant. The Asian species usually do not live as long as American chestnut. In a forest setting, the other *Castanea* species are not competitive; they do not grow tall enough or fast enough to compete for light against the native American chestnut or other native tree species (Wu and Raven, 1999; Fei et al., 2012). The American chestnut has lost the role it once had as a foundational species that influenced other species and ecosystem processes.



FIGURE 2-6 Dead American chestnut trees in Chattahoochee National Forest, 1930. PHOTO CREDIT: U.S. Forest Service.

As with many trees, the American chestnut faces more than one threat. In southern Appalachia, the introduced oomycete *Phytophthora cinnamomi* causes black lesions on the roots, eventually killing the tree by killing the root system (Crandall et al., 1945). Trials of restoration plantings in this region reveal that *P. cinnamomi* persists in the soil long after the mature chestnuts die and kills the majority of planted chestnut seedlings within a few months (Rhoades et al., 2003). Asian chestnut gall wasp (*Dryocosmus kuriphilus*), accidentally imported on Asian chestnut cuttings in 1974 (Payne et al., 1976), attacks both Asian and American chestnuts. The galls suppress shoot growth and nut development.

American chestnut is the committee's only case study of a species that has essentially been lost throughout its native range as of 2018. Oaks and maples have filled in for this species over much of the range and maintained some of the forest functions (Keever, 1953; Woods and Shanks, 1959; McCormick and Platt, 1980). Although acorns have replaced chestnuts as mast sources to some extent, oaks have episodic mast years, unlike the consistent, substantial annual mast produced by the American chestnut and chestnut's relatives, the chinquapins (*Castanea pumila* and *C. ozarkensis*). Population dynamics of species dependent on the nuts were likely affected, with cascading food web impacts. At least five moth species obligate on chestnuts have gone extinct (Opler, 1978; Wagner and Van Driesche, 2010). Economies and cultures of human communities originally reliant on American chestnut products were also altered (Davis, 2006); chestnut has been identified as a cultural keystone species (*sensu* Garibaldi and Turner, 2004).

Whitebark Pine (*Pinus albicaulis*)

Whitebark pine is a high-elevation tree of the western United States and Canada (see Figure 2-7). It spans over 18° latitude and 21° longitude, but within that area it establishes only within a narrow elevational distribution extending from the subalpine to treeline (Tomback et al., 2016). The tree exhibits high phenotypic plasticity (i.e., an ability to grow in different forms in response to its environment). In open stands, it grows as a large wide-crowned tree, whereas in dense stands it takes a linear form similar to lodgepole pine. On harsh windswept ridges, it forms krummholz—dwarfed, gnarled trees that seldom reach more than 1–2 meters in height, even when hundreds of years old. In the subalpine, it sometimes grows in mixed stands, often with subalpine fir, Engelmann spruce, and lodgepole pine. In the upper extent of the subalpine and at treeline, whitebark pine is typically the only tree present (Tomback et al., 2016). It is a long-lived tree, sometimes reaching ages of 1,000 years or more (Perkins and Swetnam, 1996). It grows slowly and typically does not begin to reproduce until at least 20–30 years of age and not fully until 60 or more years (McCaughy and Tomback, 2001).

Whitebark pine is considered to be both a keystone and a foundational species. As a keystone, its presence sustains the biodiversity and function of the community of which it is part. As a foundational species, it is responsible for creating the conditions that allow the community to assemble in the first place (Tomback et al., 2016). At the upper limits of its elevational range, whitebark pine establishes in areas too harsh to support other tree species (Weaver and Dale, 1974; Tomback and Linhart, 1990). In these places, whitebark pines provide shelter and contribute to soil development, allowing other plant species to establish (Arno and Hoff, 1990; Callaway, 1998). “Life islands” of shrubby vegetation often develop at the base of these trees, providing food and nesting habitat for birds and small mammals and stabilizing rocky slopes. Cover provided by the trees regulates snowmelt, retaining water in the subalpine for longer into the spring and supporting flows in mid and low elevations for an extended period into the summer (Farnes, 1990).

The tree is threatened by several factors including human-induced changes in fire regimes (suppression), an introduced fungal pathogen (*Cronartium ribicola*, the causal agent of a disease called white pine blister rust), a native bark beetle (the mountain pine beetle, *Dendroctonus ponderosae*), and climate change (increased drought). Individually, each threat is serious. These factors also interact, exacerbating the rate and degree of decline. Together, these threats pose an extremely complex problem for the conservation and restoration of this tree.

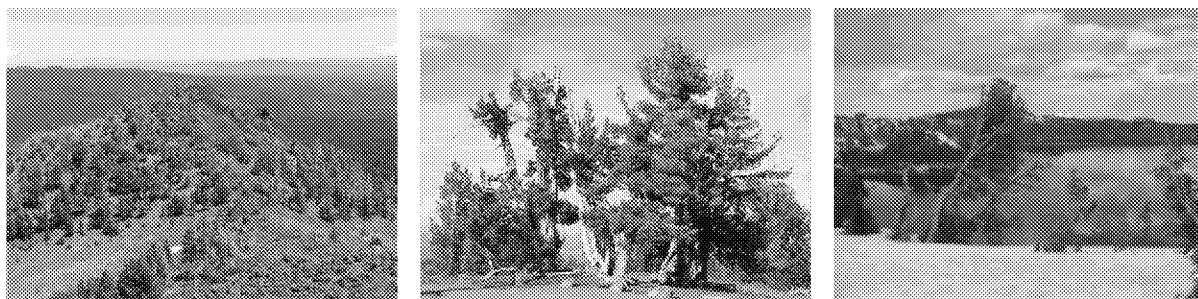


FIGURE 2-7 Whitebark pine as predominant component of high-elevation forest in southern Oregon, Umpqua National Forest (left) and Crater Lake National Park (center and right). PHOTO CREDIT: R. Snieszko.

Over half of all whitebark pine in the northern United States and Canada are already dead. In some areas, only about 2 percent of mature (reproductive) trees remain (Kendall and Keane, 2001; Zeglen, 2002; Smith et al., 2008). Seeds are dispersed by birds in the jay family, specifically Clark’s nutcrackers (*Nucifraga columbiana*), that open the cones and cache the seeds for later use. Seeds in unretrieved caches germinate to produce new whitebark pines. In areas where few mature trees remain, foraging becomes inefficient and the nutcrackers reduce visitation to these sites, thus lowering the potential for regeneration (McKinney and Tomback, 2007; McKinney et al., 2009; Barringer et al., 2012).

Mortality has been most severe in the central and northern Rocky Mountains, and in the coastal mountain ranges, whereas southern populations remain fairly robust due primarily to a lack of rust and beetle activity as of 2018. Canada listed whitebark pine as endangered in 2010 (COSEWIC, 2010). The tree’s status in the United States is “recommended for listing, but precluded” (USFWS, 2011). Preclusion, in this case, is based on a lack of funding and its lower priority for recovery relative to several other species. As of 2018, the tree’s status under the Endangered Species Act was under re-review, with a decision slated for 2019.

North American Ash (*Fraxinus* spp.)

There are 16 ash species native to North America, of which green ash (*Fraxinus pennsylvanica*) and white ash (*F. americana*) are the most widely distributed. The native range of green ash includes the Eastern Temperate, Great Plains, and Northern Forests ecoregions in North America (see Figure 2-8; CEC, 1997; Omernik, 1995, 2004; Omernik and Griffith, 2014). Although green ash grows abundantly in riparian zones in mesic temperate forests, it can persist in upland forests and seasonally dry urban environments throughout the eastern and central United States. In the Great Plains ecoregion in the western part of the range, green ash can be locally abundant in riparian zones or along ephemeral streams (Rumble and Gobeille, 1998; Lesica, 2009). Although this species occupies only 1–4% of the landscape in this region, green ash woodlands support a disproportionately large component of biological diversity, including migratory songbirds, gallinaceous birds, and native ungulates (Boldt et al., 1979; MacCracken and Uresk, 1984; Hodorff and Sieg, 1986; Rumble and Gobeille, 1998). Additionally, 43 native arthropod species are solely dependent on green and white ash during some part of their life cycle, and 30 additional species have only 2–3 known host plants, one of which is ash (Gandhi and Herms, 2010b).

First detected in Detroit, Michigan, and Windsor, Ontario, in 2002, the emerald ash borer (EAB, *Agrius planipennis* Fairmaire (Coleoptera: Buprestidae)) poses an acute threat to all of the native ash species in North America (Herms and McCullough, 2014). The International Union for Conservation of Nature Red List of Threatened Species lists five North American ash species—green ash, white ash, black ash (*F. nigra*), pumpkin ash (*F. profunda*), and blue ash (*F. quadrangulata*)—as critically endangered due to nearly 100-percent mortality following attack, limited ability to regenerate under repeated attack, and rapid spread of the insect, largely through unintentional human agency. EAB, native to Asia, had spread to 31 states and 3 Canadian provinces as of May 2018 (see Figure 2-8).

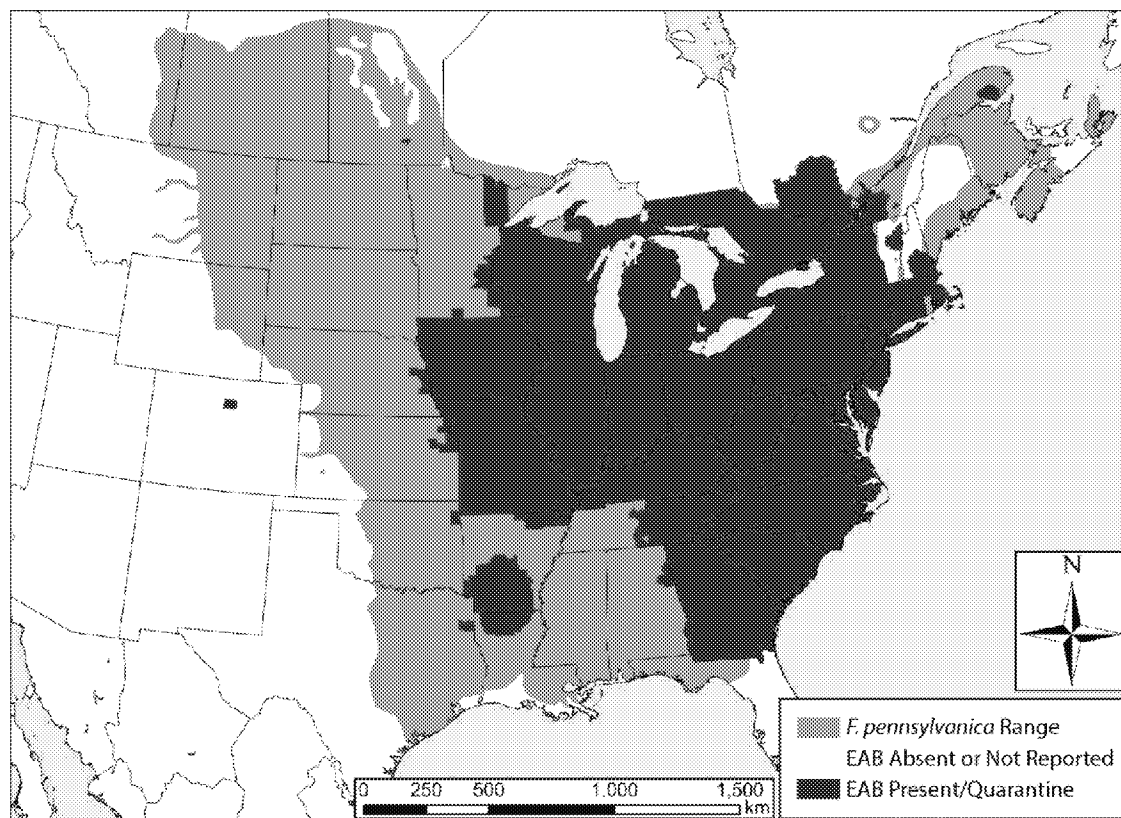


FIGURE 2-8 Range of green ash (*Fraxinus pennsylvanica*) and extent of emerald ash borer invasion as of May 17, 2018. NOTE: Planting and establishment of green ash outside the native range results in emerald ash borer infestation beyond the native range of *F. pennsylvanica*. SOURCES: Data from emerald ash borer information network <http://www.emeraldashborer.info/index.php>. Figure by Devin Shirley.

The insect kills 99–100 percent of green ash trees in forest stands within 7 years of first detection (see Figure 2-9A) and kills urban green ash plantings as fast or faster, due to the extensive use of grafted green ash cultivars (Rebek et al., 2008; Smitley et al., 2008; Knight et al., 2012). Females oviposit in bark cracks and crevices, laying 60–80 eggs. Larvae hatch in a few weeks, feed voraciously on the phloem and other living tissues under the bark and complete four instars before overwintering as prepupae (Cappaert et al., 2005). Pupation occurs in the spring and adults emerge starting in mid-May and continuing throughout the summer (Poland et al., 2011). EAB feeding destroys the vasculature and the tissue that forms new vessels and bark, ultimately girdling the main stem and thus killing the host (see Figure 2-9B).

Green ash, as well as the other ash species listed as critically endangered, has some capacity to regenerate from root and stump sprouts even after EAB infestation (Kashian, 2016). However, EAB also kills these resprouts, removing any mechanism for regeneration via vegetative propagation. Ash seedlings may be initially abundant after extensive mortality among adult trees (Kashian and Witter, 2011), giving the impression that ash will recover. However, when these seedlings reach 2–3 cm in stem diameter, EAB infestation again inflicts high mortality. Ash does not have a persistent seedbank, so once mature trees are killed, it is nearly impossible for the species to reestablish itself.



A



B

FIGURE 2-9 Ash tree mortality from emerald ash borer (EAB) damage. (A) Ash trees killed by EAB. (B) Galleries in ash tree's phloem caused by EAB larval feeding. PHOTO CREDITS: (A) R. Papps; (B) <https://www.istockphoto.com/photo/dead-tree-trunk-showing-tracks-of-emerald-ash-borer-larvae-gm936680918-256245154>.

The near synchronous loss of green ash has had a cascade of negative impacts, including the rapid loss of naturally occurring riparian forests, which are composed mainly of green or black ash (Gandhi and Herms, 2010a,b; Hausman et al., 2010; Kovacs et al., 2010; Knight et al., 2013), billions of dollars in tree removal cost to local governments, and the loss of a valuable utility hardwood used for cabinets, furniture, tool handles, restoration of antique cars, wooden snowshoes, guitars, and baseball bats. Five or more hawk moth species that specialize on *Fraxinus* are hypothesized to be at risk from the loss of ash to EAB (Wagner and Van Driesche, 2010). Thus, without effective and timely intervention, the EAB invasion threatens two of the most widely distributed hardwood species in the riparian forests of eastern North America and the

most extensively used group of tree species for soil conservation, rural water management, urban green spaces, and utility woodworking as well as the species that depend on *Fraxinus*. It also threatens to continue its spread west, where it will likely kill western species of ash that have so far been unaffected.

Poplar (*Populus* spp.)

This case study presents an example of an incipient invasion of a pathogen native to forest ecosystems in eastern North America that poses a threat to an ecologically important native tree group in western North America as well as to a sector of the forest products industry. There are eight native species of *Populus* in North America and multiple hybrids (Cooke and Rood, 2007), but the focus of the case study is on three species: black cottonwood (*P. trichocarpa*), the closely related balsam poplar (*P. balsamifera*), and widespread eastern cottonwood (*P. deltoides*) (see Figure 2-5). These species are model organisms for basic research, so in some ways this tree species may represent a best-case scenario for the potential of biotechnology to prevent or mitigate a forest health crisis.

In open environments, black cottonwood is a dominant native tree in lowland riparian ecosystems in Oregon, Washington, and British Columbia (Franklin and Dyrness, 1973), where it plays essential roles in stream ecology (Pastor et al., 2014) and as habitat for birds and mammals (Kauffman and Krueger, 1984; Isaacs et al., 1993, 1996; Bryce et al., 2002). Black cottonwood populations typically become established following deposition of sand and gravel following episodic floods, resulting in bands of even-aged cohorts that line river floodplains (Braatne et al., 1996). The species produces abundant seeds with cotton-like appendages that facilitate long-distance dispersal by wind and water (Slavov et al., 2010; DiFazio et al., 2012) and enable deposition on newly created substrates following recession of floodwaters. It also spreads vegetatively by root sprouts or abscised branches, leading to the development of large clonal stands in some locations (Gom and Rood, 1999; Slavov et al., 2010). As a result, this species is critical for floodplain soil stabilization and provides habitat for other species. Black cottonwood populations have shown evidence of decline in recent decades, in part because of a loss of establishment opportunities due to flood control (Dykaar and Wigington, 2000; Braatne et al., 2007). However, extensive gallery forests of this species are still a prominent and valued component of the landscape in the Pacific Northwest.

In research, the genus *Populus* is widely recognized as a model for woody tree biology (Taylor, 2002; Jansson and Douglas, 2007). The genus has several desirable experimental characteristics, including a small genome (Tuskan et al., 2006), easy vegetative propagation via stem cuttings and tissue culture, ability to hybridize (Induri et al., 2012), and short generation time (Stanton et al., 2010). These features have made *Populus* an attractive model for applied studies focused on enhancing productivity in intensive plantation settings for pulp, biofuel, and solid wood (Dickmann, and Kuzovkina, 2014). *Populus* spp. have also been a primary target of basic research in the areas of physiology, ecology, and evolutionary biology. Consequently, abundant genetic and genomic resources are available for this genus (Tuskan et al., 2006; Evans et al., 2014; Zinkgraf et al., 2016; Fahrenkrog et al., 2017).

The fungal pathogen *Sphaerulina musiva* (synonym, *Septoria musiva*) is native to eastern North America, with a historical distribution that largely mirrors that of its primary natural host, eastern cottonwood. The pathogen causes blotches and stem cankers in *P. deltoides*, *P. balsamifera*, *P. trichocarpa*, and hybrid *Populus* cultivars in North America (see Figure 2-10). The disease initially occurred primarily in natural populations of *P. deltoides* in the east, where it was mostly manifested as leaf spots (Waterman, 1954). However, it has since spread from eastern forests to intensively cultivated eastern plantations of native and hybrid poplars, where it commonly causes stem and branch cankers, often leading to breakage of the main stem and death of the tree (Ostry and McNabb, 1985; Dunnell et al., 2016). In the most detailed published survey of a large-scale outbreak, Strobl and Fraser (1989) documented occurrence of *S. musiva* canker in intensively cultivated hybrid poplar in Ontario. Within 5 years of the establishment of susceptible hybrid clones in the region, over 150 hectares (370 acres) of plantations were affected by the disease, and 79 percent of the area planted with susceptible clones had disease outbreaks (Strobl and Fraser, 1989). This disease can clearly have rapid and devastating impacts on intensive plantations of susceptible varieties (Feau et al., 2010).



FIGURE 2-10 *Sphaerulina musiva* canker on *Populus*. PHOTO CREDIT: S. Simon.

Of even greater concern are reports of stem cankers caused by *S. musiva* in natural populations of black cottonwood in Pacific Northwest forests, where the disease is not native and was unknown until 2006 (Callan et al., 2007; Herath et al., 2016). Both *P. trichocarpa* and *P. balsamifera* show high susceptibility to this disease (LeBoldus et al., 2013; Herath et al., 2016), so the threat of a large-scale outbreak has caused substantial concern among scientists, members of the forest industry, land managers, and the public (Feau et al., 2010). Black cottonwood may be particularly vulnerable to an outbreak of this disease. In the core of its range along rivers of northwestern North America, black cottonwood often occurs in dense, even-aged stands in climates and microsites that are characterized by abundant moisture (DiFazio et al., 2011), which could facilitate spread of the disease. Furthermore, *P. trichocarpa* populations are already in decline due to flood control and habitat loss (Rood and Mahoney, 1990; Dykaar and Wigington, 2000), so a disease outbreak could be particularly problematic for the long-term viability of the species.

Effects on Forest Health and Ecosystem Services

The case studies are not isolated examples of species in decline. Rather, given the rate of introductions of nonnative insect pests and pathogens and the effects of climate change on distribution and abundance of native insects and pathogens, their trajectory is likely to become the norm in North American forests. The frequency and magnitude of outbreaks and the rate of tree mortality are likely to increase. These impacts will have significant effects on forest health and ecosystem services (Dukes et al., 2009; Millar and Stephenson, 2015; Lovett et al., 2016; Liebhold et al., 2017). As outlined above, ecosystem services are generally defined as the direct and indirect contributions of ecosystems to human well-being (Braat and de Groot, 2012; see also the discussion in Chapter 5).

The most immediate effects of increased insect and pathogen activity (native and introduced) on forest health are reductions in productivity and alterations of nutrient, carbon, and water cycles (Lovett et al., 2006). In the case of extended or severe tree mortality, as in the American chestnut, substantial losses of other forest species and some ecosystem services can be expected.

The impact of increased insect pest and pathogen activity on ecosystem services is strongly linked to the proportion of the canopy affected. Increases in the effects of host-specific insects and pathogens that target dominant and keystone tree species will likely result in the most severe and long-term impacts (Ellison et al., 2005a). For example, eastern hemlock (*Tsuga canadensis*) dominates forest stands in its northern range and moist coves in the south. Loss of the hemlock due to the nonnative hemlock wooly adelgid (*Adelges tsugae*) has caused the loss of several wildlife species associated with hemlock (Tingley et al., 2002; Ellison et al., 2005b), affected soil processes (Jenkins et al., 1999), and changed local hydraulic flow (Ellison et al., 2005a). These impacts may occur even where other tree species rapidly colonize areas once occupied by hemlock (Orwig et al., 2002), as the ecosystem services provided by one species may differ from those provided by others. For example, in the Southern Appalachians, the effects of hemlock trees on stream flow and temperature sustain unique communities of salamanders, fish, and other stream invertebrate species (Snyder et al., 2002) that will be lost without hemlocks.

In areas of low tree diversity, outbreaks of insect pests and pathogens can have devastating consequences for regulating and supporting services, as a large proportion of the canopy can be affected with no replacement species naturally recolonizing afterward. This is the case with whitebark pine. The ecological void created by the loss of whitebark pine (see case study above) will be vast because this species supplies numerous resources, including shelter and food to wildlife species, water regulation through snowpack retention, and soil development, which facilitates the establishment of other plant species (Arno and Hoff, 1990; Farnes, 1990; Callaway, 1998).

Intrinsic properties of the ecosystem may mediate the magnitude of the loss of ecosystem services. High-diversity forests are home to more introduced insect pests and pathogens (Liebhold et al., 2013), but the loss of one tree species in these areas may be compensated by other species. For example, even though white ash (*Fraxinus americana*) is a conspicuous species in eastern North American forests, it does not dominate these stands (Prasad et al., 2007-ongoing). As of 2018, EAB was causing the death of most adult white ash trees across large areas. However, the void left by the death of ash trees is rapidly being filled by other tree species, such as maples (Margulies et al., 2017). Maples likely supply some of the ecosystem services provided by ash but may not support the biodiversity reflective of an uninvaded forest. The same was true for the eastern forest when American chestnut declined; the replacement species produce neither the mast, timber, stature, nor the cultural or spiritual values of the original forest (Davis, 2006). Additionally, while replacement species offer at least a temporary mitigation of some impacts, the continual influx of nonnative insects and pathogens could subject the replacement species themselves to impacts in the future, a factor to consider when deciding whether to try to restore species in jeopardy of extirpation.

However, even if impacts can be mostly mitigated by replacement tree species, the costs can still be substantial. Shortly after EAB was found in the United States, the Forest Service projected the lost timber value from ash trees in forested lands could be close to \$280 billion (Nowak et al., 2003). Additionally, the anticipated cost of losing these species in urban settings was estimated to be between \$20 billion and \$60 billion (USDA-APHIS, 2003) due to loss of property value and cost of removal. Using this subset of ecosystem values, the emerald ash borer is the most economically devastating invasive insect pest in North American history (Herms and McCullough, 2014).

The effects of insect pests and pathogens on individual trees have cascading impacts on populations, reducing reproduction and survival. In the most extreme cases, local extirpation of the tree species and extinction or extirpation of species dependent on the tree may result (e.g., the already mentioned extinction of five moth species with the loss of the American chestnut (Opler, 1978; Wagner and Van Driesche, 2010). Such species-specific effects can then translate into changes in community assemblage and structure, and thus, ecosystem functionality. The loss of whitebark pine may reduce the complexity and function of high-elevation ecosystems in the west and contribute to the decline of grizzlies and other wildlife as well as ecosystem services related to water and sediment regulation. The loss of ash trees affects not only natural communities; loss of city trees has had a large effect on property values (Aukema et al., 2011). The decline of black cottonwood in the West would adversely affect riparian habitats.

CONCLUSIONS

Based on its evaluation of the scientific literature and the information it gathered from invited speakers, the committee defined *forest health* as a condition that sustains the structure, composition, processes, function, productivity, and resilience of forest ecosystems over time and space. An assessment of this condition is based on the current state of knowledge and can be influenced by human needs, cultural values, and land management objectives. North American forests are struggling to maintain healthy conditions because of increasing stresses, on to which outbreaks of introduced insects and pathogens and the geographic expansion of native pests due to climate change are layered. While impossible to fully isolate, the direct adverse effects of pests on forest health have significant impacts on the ecosystem services that forests provide.

Conclusion: Healthy forests provide valuable ecosystem services to humans.

The ecological processes performed by forests and the cultural and aesthetic values attached to forests are important to individuals and to society. Forests provide food and habitat for pollinators, fish, wildlife, and other organisms, as well as food, fuel, and products for humans.

Conclusion: The health of North American forests is threatened by the introduction and spread of nonnative insects and pathogens and the epidemics of native pests exacerbated by environmental stress due to climate change.

At least 62 insect species and 16 pathogens that cause tree mortality, canopy thinning, growth loss, defoliation, or decreased reproduction or regeneration have been introduced to North America. Some of these introductions have had devastating consequences in North American forests. Increases in human mobility and trade are likely to lead to more such introductions. Climate change is opening new opportunities for colonization by both native and introduced insect species and affecting the frequency and magnitude of outbreaks of both native and introduced pests. Outbreaks are predicted to increase in frequency and magnitude in the future.

Conclusion: Tree species in forest ecosystems, tree plantations, and urban landscapes across North America are threatened by insect pests and pathogens.

The four case study species selected by the committee—American chestnut (*Castanea dentata*), whitebark pine (*Pinus albicaulis*), ash (*Fraxinus* spp.), and poplar (*Populus* spp.)—serve as examples of diverse ecosystems and habitats that are experiencing adverse impacts from tree mortality caused by insect pests and pathogens. The American chestnut was a foundation species because of its strong influence on ecosystem structure and function and an economic resource for communities before its extirpation. Whitebark pine creates and sustains community biodiversity at high elevations. Ash woodlands support biodiversity and provide benefits to humans as a popular urban landscape tree. Black cottonwood stabilizes streambanks and provides habitat for birds and mammals; poplars are also model trees for research and an important resource for production of pulp, biofuel, and solid wood.

Conclusion: Many forest tree species are threatened by more than one insect pest or pathogen.

American chestnut, whitebark pine, ash, and poplar are just four examples of North American tree species that have been or are in danger of being extirpated. They are subject to one or more pest threats, and whitebark pine, in particular, is losing habitat to climate change. The number of (see Table 2-1) and trend in (Figure 2-2) introduced threats and the geographic expanse of all pest threats represented by the four case study species (Figure 2-5) suggest that native trees throughout North America are in danger of or may become subject to pest outbreaks that adversely affect forest health.

Conclusion: As the frequency of insect and pathogen outbreaks increases, many forest tree species are in jeopardy of being lost from the landscape, resulting in changes to ecosystem services.

The growth in global trade, the increase in human mobility, and the warming of the climate are all contributing to the increased pest pressure that forests now face. The magnitude of pest outbreaks may permanently change the structure, composition, processes, function, productivity, and resilience of forest ecosystems. As tree species are lost from the landscape, the species obligate to those trees will be lost as well.

REFERENCES

- Aldred, J. 1994. Existence value, welfare and altruism. *Environmental Values* 3(4):381–402.
- Anagnostakis S.L. 1987. Chestnut blight: The classical problem of an introduced pathogen. *Mycologia* 79(1):23–37.
- Anagnostakis S.L. 2000. Revitalization of the majestic chestnut: Chestnut blight disease. APSnet Feature. Available at <http://www.apsnet.org/publications/apsnetfeatures/Pages/ChestnutBlightDisease.aspx>. Accessed August 25, 2018.
- Anagnostakis S.L., and B. Hillman. 1992. Evolution of the chestnut tree and its blight. *Arnoldia* 52(2):2–10.
- Arno, S.F. and R.J. Hoff. 1990. *Pinus albicaulis* Engelm. whitebark pine. Pp. 268–279 in *Silvics of North America* Volume 1, R.M. Burns and B.H. Honkala, tech. cords. Washington, DC: U.S. Government Printing Office.
- Aukema, J.E., B. Leung, K. Kovacs, C. Chivers, K.O. Britton, J. Englin, S.J. Frankel, R.G. Haight, T.P. Holmes, A.M. Liebhold, D.G. McCullough, and B. Von Holle. 2011. Economic impacts of non-native forest insects in the continental United States. *PLoS One* 6(9):e24587.
- Aukema, J.E., D.G. McCullough, B. Von Holle, A.M. Liebhold, K. Britton, and S.J. Frankel. 2010. Historical accumulation of nonindigenous forest pests in the continental United States. *BioScience* 60(11):886–897.
- Ayres, M.P., and M.J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment* 262(3):263–286.
- Bale, J.S., G.J. Masters, I.D. Hodkinson, C. Awmack, T.M. Bezemer, V.K. Brown, J. Butterfield, A. Buse, J.C. Coulson, J. Farrar, J.E.G. Good, R. Harrington, S. Hartley, T.H. Jones, R.L. Lindroth, M.C. Press, I. Symrnioudis, A.D. Watt, and J.B. Whittaker. 2002. Herbivory in global climate change research: Direct effects of rising temperature on insect herbivores. *Global Change Biology* 8(1):1–16.
- Barnes, B.V., and W.H. Wagner. 2004. *Michigan Trees*. Ann Arbor, MI: University of Michigan Press.
- Barringer, L.E., D.F. Tomback, M.B. Wunder, and S.T. McKinney. 2012. Whitebark pine stand condition, tree abundance, and cone production as predictors of visitation by Clark’s nutcracker. *PLoS One* 7(5):e37663.
- Battisti, A., M. Stastny, S. Netherer, C. Robinet, A. Schopf, A. Roques, and S. Larsson. 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications* 15(6):2084–2096.
- Bennett, K.P., ed. 2010. *Good Forestry in the Granite State: Recommended Voluntary Forest Management Practices for New Hampshire*. 2nd edition. Durham: University of New Hampshire Cooperative Extension.
- Bentz, B.J., J. Régnière, C.J. Fettig, E.M. Hansen, J.L. Hayes, J.A. Hicke, R.G. Kelsey, J.F. Negrón, and S.J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *BioScience* 60(8):602–613.
- Berg, E.E., J.D. Henry, C.L. Fastie, A.D. De Volder, and S.M. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management* 227(3):219–232.
- Bergot, M., E. Cloppet, V. Pérarnaud, M. Déqué, B. Marçais, and M. Desprez-Loustau. 2004. Simulation of potential range expansion of oak disease caused by *Phytophthora cinnamomi* under climate change. *Global Change Biology* 10(9):1539–1552.
- Boisvenue, C., and S.W. Running. 2006. Impacts of climate change on natural forest productivity—evidence since the middle of the 20th century. *Global Change Biology* 12(5):862–882.
- Boldt, C.E., D.W. Uresk, and K.E. Severson. 1979. Riparian woodlands in jeopardy on Northern High Plains. Pp. 184–189 in *Proceedings National Symposium on Strategies for Protection and Management of Floodplain Wetlands and Other Riparian Ecosystems*, R.F. Johnson and J.F. McCormick, eds. Washington, DC: U.S. Forest Service.
- Boyd, I.L., P.H. Freer-Smith, C.A. Gilligan, and H.C.J. Godfray. 2013. The consequence of tree pests and diseases for ecosystem services. *Science* 342:1235773.

- Braat, L.C., and R. de Groot. 2012. The ecosystem services agenda: Bridging the worlds of natural science and economics, conservation and development, and public and private policy. *Ecosystem Services* 1(1):4–15.
- Braatne, J.H., R. Jamieson, K.M. Gill, and S.B. Rood. 2007. Instream flows and the decline of riparian cottonwoods along the Yakima River, Washington, USA. *River Research and Applications* 23(3): 247–267.
- Braatne, J.H., S.B. Rood, and P.E. Heilman. 1996. Life history, ecology, and reproduction of riparian cottonwoods in North America. Pp. 57–85 in *Biology of Populus and Its Implications for Management and Conservation*, R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman, and T.M. Hinckley, eds. Ottawa, ON: NRC Research Press.
- Braun, E.L. 1950. *Deciduous Forests of Eastern North America*. New York: Hafner.
- Breshears, D.D., N.S. Cobb, P.M. Rich, K.P. Price, C.D. Allen, R.G. Balice, W.H. Romme, J.H. Kastens, M.L. Floyd, J. Belnap, J.J. Anderson, O.B. Myers, and C.W. Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America* 102(42):15144–15148.
- Brockerhoff, E.G., M. Kimberley, A.M. Liebhold, R.A. Haack, and J.F. Cavey. 2014. Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools. *Ecology* 95(3):594–601.
- Bryce, S.A., R.M. Hughes, and P.R. Kaufmann. 2002. Development of a bird integrity index: Using bird assemblages as indicators of riparian condition. *Environmental Management* 30(2):294–310.
- Burkhard, B., and J. Maes, eds. 2017. *Mapping Ecosystem Services*. Sofia: Pensoft.
- Buttrick, P.L. 1925. Chestnut in North Carolina. Pp. 6–10 in *Chestnut and the Chestnut Blight in North Carolina*. North Carolina Geological and Economic Survey: Economic Paper 56.
- Callan, B., I. Leal, B. Foord, J.J. Dennis, and C. van Oosten. 2007. *Septoria musiva* isolated from cankered stems in hybrid poplar stool beds, Fraser Valley, British Columbia. *North American Fungi* 2(7): 1–9.
- Callaway, R.M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. *Oikos* 82(3):561–573.
- Cappaert, D., D.G. McCullough, T.M. Poland, and N.W. Siegert. 2005. Emerald ash borer in North America: A research and regulatory challenge. *American Entomologist* 51(3):152–165.
- Carroll, A.L., S.W. Taylor, J. Régnière, and L. Safranyik. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. Pp. 223–232 in *Mountain Pine Beetle Symposium: Challenges and Solutions*, 30–31 October 2003, Kelowna, British Columbia, T.L. Shore, J.E. Brooks, and J.E. Stone, eds. Victoria, BC: Natural Resources Canada.
- Castlebury, L.A., A.Y. Rossman, and A.S. Hyten. 2006. Phylogenetic relationships of *Neonectria/Cylindrocarpum* on *Fagus* in North America. *Canadian Journal of Botany* 84(9):1417–1433.
- CEC (Commission for Environmental Cooperation). 1997. *Ecological Regions of North America: Toward a Common Perspective*. Montreal: CEC Secretariat.
- Cooke, J.E., and S.B. Rood. 2007. Trees of the people: The growing science of poplars in Canada and worldwide. *Botany* 85(12):1103–1110.
- Cooper, N., E. Brady, H. Steen, and R. Bryce. 2016. Aesthetic and spiritual values of ecosystems: Recognising the ontological and axiological plurality of cultural ecosystem ‘services’. *Ecosystem Services* 21(Part B):218–229.
- COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2010. *COSEWIC Assessment and Status Report on the Whitebark Pine *Pinus albicaulis* in Canada*. Ottawa: COSEWIC Secretariat.
- Crandall, B.S., G.F. Gravatt, and M.M. Ryan. 1945. Root disease of *Castanea* species and some coniferous and broad-leaf nursery stocks, caused by *Phytophthora cinnamomi*. *Phytopathology* 35:162–180.
- Davidson, M.D. 2013. On the relation between ecosystem services, intrinsic value, existence value and economic valuation. *Ecological Economics* 95:171–177.
- Davis, D.E. 2006. Historical significance of the American chestnut to Appalachian culture and ecology. Pp. 53–60 in *Restoration of American Chestnut to Forest Lands*, K.C. Steiner and J.E. Carlson, eds. Washington, DC: U.S. Department of the Interior.
- DeFries, R., S. Pagiola, W.L. Adamowicz, H.R. Akçakaya, A. Arcenas, S. Babu, D. Balk, U. Confalonieri, W. Cramer, F. Falconí, S. Fritz, R. Green, E. Gutiérrez-Espeleta, K. Hamilton, R. Kane, J. Latham, E. Matthews, T. Ricketts, T.X. Yue. 2005. Analytical approaches for assessing ecosystem condition and human well-being. Pp. 37–71 in *Ecosystems and Human Well-being: Current State and Trends, Volume 1*, R. Hassan, R. Scholes, and N. Ash, eds. Washington, DC: Island Press.
- Detwiler, S. 1915. The American chestnut tree. *American Forestry* 21(262): 957–960.
- Dickmann, D.I., and J. Kuzovkina. 2014. Poplars and willows of the world, with emphasis on silviculturally important species. Pp. 8–91 in *Poplars and Willows: Trees for Society and the Environment*, J.G. Isebrands and J. Richardson, eds. Wallingford, UK: CABI.

- DiFazio, S.P., S. Leonardi, G.T. Slavov, S.L. Garman, W.T. Adams, and S.H. Strauss. 2012. Gene flow and simulation of transgene dispersal from hybrid poplar plantations. *New Phytologist* 193(4):903–915.
- DiFazio, S.P., G.T. Slavov, and C.P. Joshi. 2011. *Populus*: A premier pioneer system for plant genomics. Pp. 1–28 in *Genetics, Genomics and Breeding of Poplar*, S.P. DiFazio, S. Joshi, and C. Cole, eds. Enfield, NH: Science Publishers.
- Dukes, J.S., J. Pontius, D. Orwig, J.R. Garnas, V.L. Rodgers, N. Brazee, B. Cooke, K.A. Theoharides, E.E. Stange, R. Harrington, J. Ehrenfeld, J. Gurevitch, M. Lerda, K. Stinson, R. Wick, and M. Ayres. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 39(2):231–248.
- Dunnell, K.L., B. Berguson, B. McMahon, and J.M. LeBoldus. 2016. Variation in resistance of *Populus nigra* to *Sphaerulina musiva* in the North-Central United States. *Plant Disease* 100(2):287–291.
- Dykaar, B.B., and P.J. Wigington. 2000. Floodplain formation and cottonwood colonization patterns on the Willamette River, Oregon, USA. *Environmental Management* 25(1):87–104.
- Early, R., B.A. Bradley, J.S. Dukes, J.J. Lawler, J.D. Olden, D.M. Blumenthal, P. Gonzalez, E.D. Grosholz, I. Ibañez, L.P. Miller, C.J.B. Sorte, and A.J. Tatem. 2016. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications* 7:12485.
- Ellison, A.M., M.S. Bank, B.D. Clinton, E.A. Colburn, K. Elliott, C.R. Ford, D.R. Foster, B.D. Kloeppel, J.D. Knoepp, G.M. Lovett, J. Mohan, D.A. Orwig, N.L. Rodenhouse, W.V. Sobczak, K.A. Stinson, J.K. Stone, C.M. Swan, J. Thompson, B. Von Holle, and J.R. Webster. 2005a. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3(9):479–486.
- Ellison, A.M., J. Chen, D. Díaz, C. Kammerer-Burnham, and M. Lau. 2005b. Changes in ant community structure and composition associated with hemlock decline in New England. Pp. 280–289 in *Proceedings of the 3rd Symposium on Hemlock Woolly Adelgid in the Eastern United States*, B. Onken and R. Reardon R, compilers. Morgantown, WV: U.S. Forest Service.
- Ellison, D., C.E. Morris, B. Locatelli, D. Sheil, J. Cohen, D. Murdiyarso, V. Gutierrez, M. Van Noordwijk, I.F. Creed, J. Pokorny, and D. Gaveau. 2017. Trees, forests and water: Cool insights for a hot world. *Global Environmental Change* 43:51–61.
- Esper, J., U. Buntgen, D.C. Frank, D. Nievergelt, and A. Liebhold. 2007. 1200 years of regular outbreaks in alpine insects. *Proceedings of the Royal Society of London B: Biological Sciences* 274(1610):671–679.
- Evans, L.M., G.T. Slavov, E. Rodgers-Melnick, J. Martin, P. Ranjan, W. Muchero, A.M. Brunner, W. Schackwitz, L. Gunter, J.-G. Chen, G.A. Tuskan, and S.P. DiFazio. 2014. Population genomics of *Populus trichocarpa* identifies signatures of selection and adaptive trait associations. *Nature Genetics* 46(10):1089–1096.
- Fahrenkrog, A.M., L.G. Neves, M.F. Resende, A.I. Vazquez, G. Campos, C. Dervinis, R. Sykes, M. Davis, R. Davenport, W.B. Barbazuk, and M. Kirst. 2017. Genome-wide association study reveals putative regulators of bioenergy traits in *Populus deltoides*. *New Phytologist* 213(2):799–811.
- Farnes, P.E. 1990. SNOTEL and snow course data: Describing the hydrology of whitebark pine ecosystems. Pp. 302–305 in *Proceedings—Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-mountain Resource*. Ogden, UT: USDA–FS.
- Feau, N., M.-J. Mottet, P. Périnet, R.C. Hamelin, and L. Bernier. 2010. Recent advances related to poplar leaf spot and canker caused by *Septoria musiva*. *Canadian Journal of Plant Pathology* 32(2):122–134.
- Fei, S., L. Liang, F.L. Paillet, K.C. Steiner, J. Fang, Z. Shen, Z. Wang, and F.V. Hebard. 2012. Modelling chestnut biogeography for American chestnut restoration. *Diversity and Distributions* 18(8):754–768.
- Fisichelli, N.A., G.W. Schuurman, and C.H. Hoffman. 2015. Is “resilience” maladaptive? Towards an accurate lexicon for climate change adaptation. *Environmental Management* 57(4):753–758.
- Franklin, J.F., and C.T. Dyrness. 1973. *Natural Vegetation of Oregon and Washington*. Portland, OR: U.S. Forest Service.
- Freinkel, S. 2009. *American Chestnut: The Life, Death, and Rebirth of a Perfect Tree*. Berkeley, CA: University of California Press.
- Gandhi, K.J.K., and D.A. Herms. 2010a. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biological Invasions* 12(2):389–405.
- Gandhi, K.J.K., and D.A. Herms. 2010b. North American arthropods at risk due to widespread *Fraxinus* mortality caused by the alien emerald ash borer. *Biological Invasions* 12(6):1839–1846.
- Garibaldi, A., and N. Turner. 2004. Cultural keystone species: Implications for ecological conservation and restoration. *Ecology and Society* 9(3).

- Glitzenstein, J.S., P.A. Harcombe, and D.R. Streng. 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. *Ecological Monographs* 56(3):243–258.
- Gom, L.A., and S.B. Rood. 1999. Patterns of clonal occurrence in a mature cottonwood grove along the Oldman River, Alberta. *Canadian Journal of Botany* 77(8):1095–1105.
- Griffin, G.J. 2000. Blight control and restoration of the American chestnut. *Journal of Forestry* 98(2):22–27.
- Haack, R. 2006. Exotic bark- and wood-boring Coleoptera in the United States: Recent establishments and interceptions. *Canadian Journal of Forest Research* 36(2):269–288.
- Haack, R.A., K.O. Britton, E.G. Brockerhoff, J.F. Cavey, L.J. Garrett, M. Kimberley, F. Lowenstein, A. Nuding, L.J. Olson, J. Turner, and K.N. Vasilaky. 2014. Effectiveness of the International Phytosanitary Standard ISPM No. 15 on reducing wood borer infestation rates in wood packaging material entering the United States. *PLoS One* 9(5):e96611.
- Hajek, A.E., B.P. Hurley, M. Kenis, J.R. Garnas, S.J. Bush, M.J. Wingfield, J.C. Van Lenteren, and M.J. Cock. 2016. Exotic biological control agents: A solution or contribution to arthropod invasions? *Biological Invasions* 18(4):953–969.
- Harvell, C.D., C.E. Mitchell, J.R. Ward, S. Altizer, A.P. Dobson, R.S. Ostfeld, and M.D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296(5576):2158–2162.
- Hausman, C.E., J.F. Jaeger, and O.J. Rocha. 2010. Impacts of the emerald ash borer (EAB) eradication and tree mortality: Potential for a secondary spread of invasive plant species. *Biological Invasions* 12(7):2013–2023.
- Helms, J.A. 1998. *The Dictionary of Forestry*. Bethesda, MD: Society of American Foresters.
- Hepting, G.H. 1974. Death of the American chestnut. *Forest & Conservation History* 18(3):60–67.
- Herath, P., S. Beauseigle, B. Dhillon, D.I. Ojeda, G. Bilodeau, N. Isabel, M.C. Gros-Louis, H. Kope, S. Zeglen, R.C. Hamelin, and N. Feau. 2016. Anthropogenic signature in the incidence and distribution of an emerging pathogen of poplars. *Biological invasions* 18(4):1147–1161.
- Hermes, D.A., and D.G. McCullough. 2014. Emerald ash borer invasion of North America: History, biology, ecology, impacts, and management. *Annual Review of Entomology* 59:13–30.
- Hodorff, R.A., and C.H. Sieg. 1986. Bird species associated with green ash woodlands in the Slim Buttes, South Dakota. *South Dakota Bird Notes* 38(3):56–60.
- Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4(1):1–23.
- Houston, D.R., and H.T. Valentine. 1988. Beech bark disease: The temporal pattern of cankering in aftermath forests of Maine. *Canadian Journal of Forest Research* 18(1):38–42.
- Induri, B.R., D.R. Ellis, G.T. Slavov, T. Yin, X. Zhang, W. Muchero, G.A. Tuskan, and S.P. DiFazio. 2012. Identification of quantitative trait loci and candidate genes for cadmium tolerance in populus. *Tree Physiology* 32(5):626–638.
- Isaacs, F.B., R.G. Anthony, M. Vander Heyden, C.D. Miller, and W. Weatherford. 1996. Habits of bald eagles wintering along the upper John Day River, Oregon. *Northwest Science* 70(1):1–9.
- Isaacs, F.B., R. Goggans, R.G. Anthony, and T. Bryan. 1993. Habits of bald eagles wintering along the Crooked River, Oregon. *Northwest Science* 67(2):55–62.
- IPCC (Intergovernmental Panel on Climate Change) 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley, eds. Cambridge and New York: Cambridge University Press.
- Jansson, S., and C.J. Douglas. 2007. *Populus*: A model system for plant biology. *Annual Review of Plant Biology* 58:435–458.
- Jenkins, J., J.D. Aber, and C.D. Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. *Canadian Journal of Forest Research* 29(5):630–645.
- Johnson, R. 2013. Growing Chestnut Trees and Hope in Western North Carolina. Available at <https://www.fs.usda.gov/detail/nfsnc/home/?cid=STELPRDB5439130>. Accessed September 15, 2018.
- Kashian, D.M. 2016. Sprouting and seed production may promote persistence of green ash in the presence of the emerald ash borer. *Ecosphere* 7(4):e01332.
- Kashian, D.M., and J.A. Witter. 2011. Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. *Forest Ecology and Management* 261(3):480–488.
- Kauffman, J.B., and W.C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications... a review. *Journal of Range Management* 37(5):430–438.
- Keane, R.M., and M.J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17(4):164–170.

- Keeton, W.S., and J.F. Franklin. 2005. Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? *Ecological Monographs* 75(1):103–118.
- Keever, C. 1953. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains. *Ecology* 34(1):44–54.
- Kendall, K.C., and Keane, R.E. 2001. Whitebark pine decline: Infection, mortality, and population trends. Pp. 221–242 in *Whitebark Pine Communities: Ecology and Restoration*, D.F. Tomback, S.F. Arno, and R.E. Keane, eds. Washington, DC: Island Press.
- Kendra, P.E., W.S. Montgomery, J. Niogret, and N.D. Epsky. 2013. An uncertain future for American Lauraceae: A lethal threat from redbay ambrosia beetle and laurel wilt disease (a review). *American Journal of Plant Sciences* 4(3):727–738.
- Knight, K.S., D. Herms, R. Plumb, E. Sawyer, D. Spalink, E. Pisarczyk, B. Wiggin, R. Kappler, and K. Menard. 2012. Dynamics of surviving ash (*Fraxinus* spp.) populations in areas long infested by emerald ash borer (*Agrilus planipennis*). Pp. 143–152 in *Proceedings of the 4th International Workshop on Genetics of Host–Parasite Interactions in Forestry*, R.A. Snieszko, A.D. Yanchuk, J.T. Kliejunas, K.M. Palmieri, J.M. Alexander, and S.J. Frankels, eds. Albany, CA: U.S. Forest Service.
- Knight, K.S., J.P. Brown, and R.P. Long. 2013. Factors affecting the survival of ash (*Fraxinus* spp.) trees infested by emerald ash borer (*Agrilus planipennis*). *Biological Invasions* 15(2):371–383.
- Kolb, T.E., M.R. Wagner, and W.W. Covington. 1994. Forest health from different perspectives. Pp. 5–13 in *Forest Health Through Silviculture: Proceedings of the 1995 National Silviculture Workshop*, L.G. Eskew, comp. Fort Collins, CO: U.S. Forest Service.
- Kovacs, K.F., R.G. Haight, D.G. McCullough, R.J. Mercader, N.W. Siegert, and A.M. Liebhold. 2010. Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. *Ecological Economics* 69(3):569–578.
- Krist, F.J., J.R. Ellenwood, M.E. Woods, A.J. McMahan, J.P. Cowardin, D.E. Ryerson, F.J. Sapio, M.O. Zweifler, and S.A. Romero. 2014. 2013–2027 National Insect and Disease Forest Risk Assessment. Fort Collins, CO: U.S. Forest Service.
- Landsberg, J.J., and R.H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management* 95(3):209–228.
- Latijnhouwers, M., P.J.G.M. de Wit, and F. Govers. 2003. Oomycetes and fungi: Similar weaponry to attack plants. *Trends in Microbiology* 11(10):462–469.
- LeBoldus, J.M., N. Isabel, K.D. Floate, P. Blenis, and B.R. Thomas. 2013. Testing the “hybrid susceptibility” and “phenological sink” hypotheses using the *P. balsamifera* - *P. deltoides* hybrid zone and *Septoria* leaf spot [*Septoria musiva*]. *PLoS One* 8(12):e84437.
- Lesica, P. 2009. Can regeneration of green ash (*Fraxinus pennsylvanica*) be restored in declining woodlands in eastern Montana? *Rangeland Ecology & Management* 62(6):564–571.
- Liebhold, A.M., E.G. Brockerhoff, S. Kalisz, M.A. Nuñez, D.A. Wardle, and M.J. Wingfield. 2017. Biological invasions in forest ecosystems. *Biological Invasions* 19(11):3437–3458.
- Liebhold, A.M., D.G. McCullough, L.M. Blackburn, S.J. Frankel, B. Von Holle, and J.E. Aukema. 2013. A highly aggregated geographical distribution of forest pest invasions in the USA. *Diversity and Distributions* 19(9):1208–1216.
- Liebhold, A.M., E.G. Brockerhoff, L.J. Garrett, J.L. Parke, and K.O. Britton. 2012. Live plant imports: The major pathway for forest insect and pathogen invasions of the US. *Frontiers in Ecology and the Environment* 10(3):135–143.
- Liebhold, A.M., W.L. MacDonald, D. Bergdahl, and V.C. Mastro. 1995. Invasion by exotic forest pests: A threat to forest ecosystems. *Forest Science Monographs* 30:1–49.
- Little, E.L., Jr., 1977. *Atlas of United States Trees, Volume 4, Minor Eastern Hardwoods*. Washington, DC: U.S. Department of Agriculture.
- Logan, J.A., J. Régnière, and J.A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* 1(3):130–137.
- Lovett, G.M., M. Weiss, A.M. Liebhold, T.P. Holmes, B. Leung, K.F. Lambert, D.A. Orwig, F.T. Campbell, J. Rosenthal, D.G. McCullough, R. Wildova, M.P. Ayres, C.D. Canham, D.R. Foster, S.L. LaDeau, and T. Weldy. 2016. Nonnative forest insects and pathogens in the United States: Impacts and policy options. *Ecological Applications* 26(5):1437–1455.
- Lovett, G.M., C.D. Canham, M.A. Arthur, R.D. Fitzhugh, and K.C. Weathers. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. *BioScience* 56(5):395–405.
- Ludwig, D., D.D. Jones, and C.S. Holling. 1978. Qualitative analysis of insect outbreak systems: The spruce budworm and forest. *Journal of Animal Ecology* 47(1):315–332.

- McCaughey, W.W., and D.F. Tomback. 2001. The natural regeneration process. Pp. 105–120 in *Whitebark Pine Communities: Ecology and Restoration*, D.F. Tomback, S.F. Arno, and R.E. Keane, eds. Washington, DC: Island Press.
- MacCracken, J.G., and D.W. Uresk. 1984. Big game habitat use in southeastern Montana. *The Prairie Naturalist* 16(3):135–139.
- Margulies, E., L. Bauer, and I. Ibáñez. 2017. Buying time: Preliminary assessment of biocontrol in the recovery of native forest vegetation in the aftermath of the invasive emerald ash borer. *Forests* 8(10):369.
- McCormick, J.F., and R.B. Platt. 1980. Recovery of an Appalachian forest following the chestnut blight or Catherine Keever—you were right! *American Midland Naturalist* 104(2):264–273.
- McKinney, S.T., and D.F. Tomback. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. *Canadian Journal of Forest Research* 37(6):1044–1057.
- McKinney, S.T., C.E. Fiedler, and D.F. Tomback. 2009. Invasive pathogen threatens bird–pine mutualism: Implications for sustaining a high-elevation ecosystem. *Ecological Applications* 19(3):597–607.
- Meddens, A.J., J.A. Hicke, and C.A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications* 22(7):1876–1891.
- Milcu, A.I., J. Hanspach, D. Abson, and J. Fischer. 2013. Cultural ecosystem services: A literature review and prospects for future research. *Ecology and Society* 18(3):44.
- Millar, C.I., and N.L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349(6250):823–826.
- Moore, R. 2004. Forest vegetation. Pp. 3.2-1–3.2-84 in *Final Environmental Impact Statement for Forest Plan Revision, Chippewa National Forest, Superior National Forest*. Available at https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsm91_048435.pdf. Accessed August 23, 2018.
- Moser, W.K., E.L. Barnard, R.F. Billings, S.J. Crocker, M.E. Dix, A.N. Gray, G.G. Ice, M.S. Kim, R. Reid, S.U. Rodman, and W.H. McWilliams. 2009. Impacts of nonnative invasive species on US forests and recommendations for policy and management. *Journal of Forestry* 107(6):320–327.
- NRC (National Research Council). 2005. *Valuing Ecosystem Services: Toward Better Environmental Decision-Making*. Washington, DC: The National Academies Press.
- Nowak, D., D. Crane, J. Stevens, and J. Walton. 2003. *Potential Damage from Emerald Ash Borer*. Syracuse, NY: U.S. Forest Service.
- Nowak, D. J., S. Hirabayashi, A. Bodine, and E. Greenfield. 2014. Tree and forest effects on air quality and human health in the United States. *Environmental Pollution* 193:119–129.
- Olander, L., R.J. Johnston, H. Tallis, J. Kagan, L. Maguire, S. Polasky, D. Urban, J. Boyd, L. Wainger, M. Palmer. 2015. *Best Practices for Integrating Ecosystem Services into Federal Decisionmaking*. Durham, NC: National Ecosystem Services Partnership, Duke University.
- Omernik, J.M. 1995. Ecoregions: A spatial framework for environmental management. Pp. 49–62 in *Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making*. Boca Raton, FL: Lewis.
- Omernik, J.M. 2004. Perspectives on the nature and definition of ecological regions. *Environmental Management* 34(1):S27–S38.
- Omernik, J.M., and G.E. Griffith. 2014. Ecoregions of the conterminous United States: Evolution of a hierarchical spatial framework. *Environmental Management* 54(6):1249–1266.
- Opler, P.A., 1978. Insects of American chestnut: Possible importance and conservation concern. Pp. 83–85 in *Proceedings of the American Chestnut Symposium*, W.L. MacDonald, F.C. Cech, J. Luchok, and C. Smith, eds. Morgantown: West Virginia University.
- Orwig, D.A., D.R. Foster, and D.L. Mause. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *Journal of Biogeography* 29(10–11):1475–1487.
- Ostry, M.E., and H.S. McNabb, Jr. 1985. Susceptibility of *Populus* species and hybrids to disease in the north central united states. *Plant Disease* 69(9):755–757.
- Paillet, F.L. 2002. Chestnut: History and ecology of a transformed species. *Journal of Biogeography* 29(10–11):1517–1530.
- Paquette, A., J. Vayreda, L. Coll, C. Messier, and J. Retana. 2018. Climate change could negate positive tree diversity effects on forest productivity: A study across five climate types in Spain and Canada. *Ecosystems* 21(5):960–970.
- Pastor, A., Z.G. Compson, P. Dijkstra, J.L. Riera, E. Martí, F. Sabater, B.A. Hungate, and J.C. Marks. 2014. Stream carbon and nitrogen supplements during leaf litter decomposition: Contrasting patterns for two foundation species. *Oecologia* 176(4):1111–1112.
- Payne, J.A., R.A. Green, and C.D. Lester. 1976. New nut pest: An Oriental chestnut gall wasp in North America. *Annual Report of the Northern Nut Growers* 67:83–86.

- Perkins, D.L., and T.W. Swetnam. 1996. A dendroecological assessment of whitebark pine in the Sawtooth–Salmon River region, Idaho. *Canadian Journal of Forest Research* 26(12):2123–2133.
- Perry, D.A. 1994. *Forest Ecosystems*. Baltimore: John Hopkins University Press.
- Poland, T.M., D.G. McCullough, and A.C. Anulewicz. 2011. Evaluation of double-decker traps for emerald ash borer (Coleoptera: Buprestidae). *Journal of Economic Entomology* 104(2):517–531.
- Prasad, A.M., L.R. Iverson, S. Matthews, and M. Peters. 2007-ongoing. A Climate Change Atlas for 134 Forest Tree Species of the Eastern United States [database]. Available at <http://www.nrs.fs.fed.us/atlas/tree>. Accessed December 8, 2018.
- Pyšek, P., V. Jarosik, P.E. Hulme, I. Kuhn, J. Wild, M. Arianoutsou, S. Bacher, F. Chiron, V. Didziulis, F. Essl, P. Genovesi, F. Gherardi, M. Hejda, S. Kark, P.W. Lambdon, M.-L. Desprez-Loustau, W. Nentwig, J. Pergl, K. Poboljsaj, W. Rabitsch, A. Roques, D.B. Roy, S. Shirley, W. Solarz, M. Vila, and M. Winter. 2010. Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America* 107(27):12157–12162.
- Raffa, K.F., B. Aukema, B.J. Bentz, A. Carroll, N. Erbilgin, D.A. Herms, J.A. Hicke, R.W. Hofstetter, S. Katovich, B.S. Lindgren, J. Logan, W. Mattson, A.S. Munson, D.J. Robison, D.L. Six, P.C. Tobin, P.A. Townsend, and K.F. Wallin. 2009. A literal use of “forest health” safeguards against misuse and misapplication. *Journal of Forestry* 107(5):276–277.
- Raffa, K.F., E.N. Powell, and P.A. Townsend. 2013. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proceedings of the National Academy of Sciences of the United States of America* 110(6):2193–2198.
- Rebek, E.J., D.A. Herms, and D.R. Smitley. 2008. Interspecific variation in resistance to emerald ash borer (Coleoptera: Buprestidae) among North American and Asian ash (*Fraxinus* spp.). *Environmental Entomology* 37(1):242–246.
- Reyer, C.P., S. Bathgate, K. Blennow, J.G. Borges, H. Bugmann, S. Delzon, S.P. Faias, J. Garcia-Gonzalo, B. Gardiner, J.R. Gonzalez-Olabarria, C. Gracia, J.G. Hernández, S. Kellomäki, K. Kramer, M.J. Lexer, M. Linder, E. van der Maaten, M. Maroschek, B. Muys, B. Nicoll, M. Pahali, J.H.N. Palma, J.A. Paulo, H. Peltola, T. Pukkala, W. Rammer, D. Ray, S. Sabaté, M.-J. Schelhaas, R. Seidl, C. Temperli, M. Tomé, R. Yousefpour, N.E. Zimmermann, and M. Hanewinkel. 2017. Are forest disturbances amplifying or canceling out climate change-induced productivity changes in European forests? *Environmental Research Letters* 12(3):034027.
- Rhoades, C.C., S.L. Brosi, A.J. Dattilo, and P. Vincelli. 2003. Effect of soil compaction and moisture on incidence of phytophthora root rot on American chestnut (*Castanea dentata*) seedlings. *Forest Ecology and Management* 184(1):47–54.
- Rolston, H. 1988. *Environmental Ethics: Duties to and Values in the Natural World*. Philadelphia: Temple University Press.
- Rood, S.B., and J.M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: Probable causes and prospects for mitigation. *Environmental Management* 14(4):451–464.
- Rumble, M.A., and J.E. Gobeille. 1998. Bird community relationships to succession in green ash (*Fraxinus pennsylvanica*) woodlands. *The American Midland Naturalist* 140(2):372–381.
- Russell, E.W.B. 1987. Pre-blight distribution of *Castanea dentata* (Marsh.) Borkh. *Bulletin of the Torrey Botanical Club* 114(2):183–190.
- Sambaraju, K.R., A.L. Carroll, J. Zhu, K. Stahl, R.D. Moore, and B.H. Aukema. 2012. Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. *Ecography* 35(3):211–223.
- Sandler, R. 2012. Intrinsic value, ecology, and conservation. *Nature Education Knowledge* 3(10):4.
- Sandler, R. 2018. Forest biotechnology: Environmental ethics perspectives. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, March 12.
- Seidl, R., T.A. Spies, D.L. Peterson, S.L. Stephens, and J.A. Hicke. 2016. Searching for resilience: Addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology* 53(1):120–129.
- Shvidenko, A., C.V. Barber, and R. Persson. 2005. Forest and woodland systems. Pp. 587–621 in *Ecosystems and Human Well-being: Current State and Trends, Volume 1*, R. Hassan, R. Scholes, and N. Ash, eds. Washington, DC: Island Press.
- Slavov, G.T., S. Leonardi, W.T. Adams, S.H. Strauss, and S.P. DiFazio. 2010. Population substructure in continuous and fragmented stands of *Populus trichocarpa*. *Heredity* 105(4):348–357.
- Smith, C.M., B. Wilson, S. Rasheed, and B. Shephard. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. *Canadian Journal of Forest Research* 38(5):982–995.

- Smitley, D., T. Davis, and E. Rebek. 2008. Progression of ash canopy thinning and dieback outward from the initial infestation of emerald ash borer (Coleoptera: Buprestidae) in southeastern Michigan. *Journal of Economic Entomology* 101(5):1643–1650.
- Snyder, C.D., J.A. Young, D.P. Lemarié, and D. Smith 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Canadian Journal of Fisheries and Aquatic Sciences* 59(2):262–275.
- Soulé, M.E. 1985. What is conservation biology? *Bioscience* 35(11):727–734.
- Stanton, B.J., D.B. Neale, and S. Li. 2010. *Populus* breeding: From the classical to the genomic approach. Pp. 309–348 in *Genetics and Genomics of Populus*, S. Jansson, R. Bhalerao, and A. Groover, eds. New York: Springer New York.
- Stephanson, C.A., and N.R. Coe. 2017. Impacts of beech bark disease and climate change on American beech. *Forests* 8(5):155.
- Stoddard, E.M., and A.E. Moss. 1913. The Chestnut Bark Disease, Bulletin 178. New Haven: The Connecticut Agricultural Experiment Station.
- Strobl, S., and K. Fraser. 1989. Incidence of Septoria canker of hybrid poplars in eastern Ontario. *Canadian Plant Disease Survey* 69(2):109–112.
- Sturrock, R.N., S.J. Frankel, A.V. Brown, P E. Hennon, J.T. Kliejunas, K.J. Lewis, J J. Worrall, and A.J. Woods. 2012. Climate change and forest diseases: Using today’s knowledge to address future challenges. *Forest Systems* 21(2):329–336.
- Taylor, G. 2002. *Populus*: Arabidopsis for forestry. Do we need a model tree? *Annals of Botany* 90(6):681–689.
- Taylor, P. 1986. *Respect for Nature*. Princeton, NJ: Princeton University Press.
- Tingley, M.W., D.A. Orwig, R. Field, and G. Motzkin. 2002. Avian response to removal of a forest dominant: Consequences of hemlock woolly adelgid infestations. *Journal of Biogeography* 29(10–11):1505–1516.
- Tomback, D.F., L.M. Resler, R.E. Keane, E.R. Pansing, A.J. Andrade, and A.C. Wagner. 2016. Community structure, biodiversity, and ecosystem services in treeline whitebark pine communities: Potential impacts from a non-native pathogen. *Forests* 7(1):21.
- Tomback, D.F., and Y.B. Linhart. 1990. The evolution of bird-dispersed pines. *Evolutionary Ecology* 4(3):185–219.
- Trumbore, S., P. Brando, and H. Hartmann. 2015. Forest health and global change. *Science* 349(6250):814–818.
- Tuskan, G.A., S. DiFazio, S. Jansson, J. Bohlmann, I. Grigoriev, U. Hellsten, N. Putnam, S. Ralph, S. Rombauts, A. Salamov, J. Schein, L. Sterck, A. Aerts, R.R. Bhalerao, R.P. Bhalerao, D. Blaudez, W. Boerjan, A. Brun, A. Brunner, V. Busov, M. Campbell, J. Carlson, M. Chalot, J. Chapman, G.-L. Chen, D. Cooper, P.M. Coutinho, J. Couturier, S. Covert, Q. Cronk, R. Cunningham, J. Davis, S. Degroove, A. Déjardin, C. DePamphilis, J. Detter, B. Dirks, I. Dubchak, S. Duplessis, J. Ehlting, B. Ellis, K. Gendler, D. Goodstein, M. Gribskov, J. Grimwood, A. Groover, L. Gunter, B. Hamberger, B. Heize, Y. Helaruitta, B. Henrissat, D. Holligan, R. Holt, W. Huang, N. Islam-Faridi, S. Jones, M. Jones-Rhodes, R. Jorgensen, C. Joshi, J. Kangasjärvi, J. Karlsson, C. Kelleher, R. Kirkpatrick, M. Kirst, A. Kohler, U. Kalluri, F. Larimer, J. Leebens-Mack, J.-C. Leplé, P. Locascio, Y. Lou, S. Lucas, F. Martin, B. Montanini, C. Napoli, D.R. Nelson, C. Nelson, K. Nieminen, O. Nilsson, V. Pereda, G. Peter, R. Phillippe, G. Pilate, A. Poliakov, J. Razumovskaya, P. Richardson, C. Rinaldi, K. Ritland, P. Rouzé, D. Rayboy, J. Schmutz, J. Schrader, B. Segerman, H. Shin, A. Siddiqui, F. Sterky, A. Terry, C.-J. Tsai, E. Uberbacher, P. Unneberg, J. Vahala, K. Wall, S. Wessler, G. Yang, T. Yin, C. Douglas, M. Marra, G. Sandberg, Y. Van de Peer, and D. Rokhsar. 2006. The genome of black cottonwood, *Populus trichocarpa* (Yorr. & Gray). *Science* 313(5793):1596–1604.
- USDA-APHIS (U.S. Department of Agriculture Animal and Plant Health Inspection Service). 2003. Emerald ash borer; Quarantine and regulations. *Federal Register* 68:59082–59091. Available at <https://www.federalregister.gov/articles/2003/10/14/03-25881/emerald-ashborer-quarantine-and-regulations>. Accessed June 29, 2018.
- USDA-FS (U.S. Department of Agriculture U.S. Forest Service). 2009. Forest Health Protection Business Plan. Arlington, VA: USDA–FS.
- USFWS (U.S. Fish and Wildlife Service). 2011. Endangered and threatened wildlife and plants: 12-month finding on a petition to list *Pinus albicaulis* as endangered or threatened with critical habitat. *Federal Register* 76:42631–42654.
- Venette, R.C. 2009. Implication of global climate change on the distribution and activity of *Phytophthora ramorum*. Pp. 58–59 in *Proceedings of the 20th U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and Other Invasive Species, 2009*, K.A. McManus and K.W. Gottschalk, eds. Newtown Square, PA: U.S. Forest Service.
- Venette, R.C., and S.D. Cohen. 2006. Potential climatic suitability for establishment of *Phytophthora ramorum* within the contiguous United States. *Forest Ecology and Management* 231:18–26.

- von Gadow, K., C.Y. Zhang, X.H. Zhao, C. Wehenkel, J. Corral-Rivas, A. Pommerening, M. Korol, S. Myklush, G.Y. Hui, and A. Kiviste. 2012. Forest structure and diversity. Pp. 29–84 in *Continuous Cover Forestry*, T. Pukkala and K. von Gadow, eds. New York: Springer.
- Wagner, D.L., and R.G. Van Driesche. 2010. Threats posed to rare or endangered insects by invasions of nonnative species. *Annual Review of Entomology* 55:547–568.
- Walker, B., C.S. Holling, S.R. Carpenter, and A. Kinzig. 2004. Resilience, adaptability, and transformability in social-ecological systems. *Ecology and Society* 9(2):5.
- Wang, G.G., B.O. Knapp, S.L. Clark, and B.T. Mudder. 2013. *The Silvics of Castanea dentata* (Marsh.) Borkh., American Chestnut, Fagaceae (Beech Family). Asheville, NC: U.S. Forest Service.
- Waterman, A.M. 1954. *Septoria Canker of Poplars in the United States*. Washington, DC: U.S. Department of Agriculture.
- Weaver, T., and D. Dale. 1974. *Pinus albicaulis* in central Montana: Environment, vegetation and production. *The American Midland Naturalist* 92(1):222–230.
- Weed, A.S., M.P. Ayres, and J.A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs* 83(4):441–470.
- Williams, D.W., and A. Liebhold. 1997. Latitudinal shifts in spruce budworm (Lepidoptera: Tortricidae) outbreaks and spruce-fir forest distributions with climate change. *Acta Phytopathologica et Entomologica Hungarica* 32(1–2):205–215.
- Wingfield, M.J., J.R. Garnas, A. Hajek, B.P. Hurley, Z.W. de Beer, and S.J. Taerum. 2016. Novel and co-evolved associations between insects and microorganisms as drivers of forest pestilence. *Biological Invasions* 18(4):1045–1056.
- Woods, F.W., and R.E. Shanks. 1959. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. *Ecology* 40(3):349–361.
- Wu, Z., and P. Raven. 1999. *Flora of China Vol 4*. Beijing and St. Louis, MO: Science Press and Missouri Botanical Garden Press.
- Youngs, R.L. 2000. “A right smart little jolt”: Loss of the chestnut and a way of life. *Journal of Forestry* 98(2):17–21.
- Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. *Canadian Journal of Forest Research* 32(7):1265–1274.
- Zinkgraf, M., K. Haiby, M.C. Lieberman, L. Comai, I.M. Henry, and A. Groover. 2016. Creation and genomic analysis of irradiation hybrids in *Populus*. *Current Protocols in Plant Biology* 1(2):431–450.
- Zvereva, E.L., V. Lanta, and M.V. Kozlov. 2010. Effects of sap-feeding insect herbivores on growth and reproduction of woody plants: A meta-analysis of experimental studies. *Oecologia* 163(4):949–960.

Mitigating Threats to Forest Health

There are multiple options for dealing with forest insect pests and pathogens, but feasibility and success vary widely. To assess the unique challenges and opportunities that a biotech tree may present as a tool for addressing forest health, it is important to understand the other options available. Given the spatial and temporal nature of forest health threats from insect pests and pathogens, it is also likely that a combination of approaches might be needed to ensure proper management of an infestation. The most cost-effective approach for protecting forest health from nonnative insect pests and pathogens (Finnoff et al., 2007) is to prevent introduction, followed by early eradication after arrival (Liebhold et al., 2016). Once established, the impact and cost of dealing with the infestation rapidly increase (Roy et al., 2014). Given that human mobility and trade volumes—major drivers of pest introductions—are likely to continue to rise, the enforcement and enhancement of preventive measures will become even more critical (Lovett et al., 2016). Even where prevention or eradication has been successful, forests will remain vulnerable to repeated introductions of the same nonnative insect pests and pathogens over time.

Once established and spreading in forests, whether pests are native or nonnative, multiple management options may exist. Management can focus on trying to minimize the damage and mortality to the forests (including the large, old-growth trees), on actively preparing to regenerate or restore a species, or on both strategies. If the impacts are not severe enough to alter the species' ecological footprint or management actions appear unrealistic or undesirable, managers may decide that taking no action is the best alternative. However, if the decision is to take action, the focus turns to early detection and response, containment, and long-term management to restrict further expansion and impact (Liebhold et al., 2017). Management options include biological control and integrated pest management, and various forms of site management (e.g., pesticide use, containment, fire, thinning) (Liebhold et al., 2017). When outbreaks of insect pests and diseases affect only one or a few tree species, the larger impact of such pests is directly related to the dominance of the host species. Thus, maintaining high levels of diversity may be an effective management approach to minimize impact. In low-diversity forests, other approaches may be more important.

In many of the most extreme cases, because of the high susceptibility of native tree species to some nonnative insects and pathogens with substantial dispersal potential, it will not be possible to prevent extremely high mortality in the affected tree species. Once an insect or pathogen is established, there are a number of key management tools that might be considered to retain the presence of the tree species in North American forests into the future. These include (1) the enhancement of genetic resistance, (2) the development and use of biocontrol agents, (3) the development and use of chemical control methods, and (4) management practices to prevent or decrease the infestation. The enhancement and use of genetic resistance can proceed through the development and deployment of selective-resistance breeding within either the native species or from closely related nonnative species or the development and deployment of resistance using biotechnology.

The effectiveness of these varied approaches to prevent and manage insect pests and pathogens varies across systems and infestations (Lovett et al., 2016). The time line for use of these tools in management activities for forest trees and forest health will depend on a number of factors, but the biology of the species involved (both tree and insect or pathogen) and the environments in which the tree species exist will have a major influence. Insecticides and fungicides are often used in attempts to preserve existing forest stands

or to protect large individual trees in urban settings. They are usually expensive, may have negative environmental impacts, and in some cases provide only a stopgap measure to give time to consider or develop other alternatives or the hope that future environmental conditions become less conducive for the damaging insect or pathogen. The same can often be said of many biological control agents. This chapter provides an overview of the different approaches and the approximate time required for implementation. The case study species are featured to illustrate the differences between species and considerations of the merits of different approaches.

PREVENTING INTRODUCTIONS

Preventing the introduction of insect pests and pathogens yields the largest ecological and economic benefits (see Figure 3-1; e.g., Mack et al., 2000; GAO, 2015). International trade agreements include clauses aimed at reducing these introductions (Burgiel et al., 2006). These are being implemented by the Animal and Plant Health Inspection Service (APHIS) of the U.S. Department of Agriculture (USDA) and include quarantine, interception (e.g., inspection, decontamination), and pre-border treatments (e.g., fumigation, immersion, spraying, irradiation, extreme temperatures) at the point of origin and during shipment (Haack et al., 2014; Leung et al., 2014).

The International Standards for Phytosanitary Measures Protocol 15 (ISPM-15) were developed under the International Plant Protection Convention to reduce the movement of wood-boring insects in pallets and other wooden shipping materials (Haack et al., 2014). Wood borers are among the most serious of insect pest invaders: 58 species of wood borers became established in the United States between 1909 and 2008 (Leung et al., 2014). The approved methods for wood treatment in the United States include heat treatment (conventional and dielectric) and fumigation with methyl bromide. An economic analysis by Leung et al. (2014) concluded that implementation of ISPM-15, though expensive and not fully effective, would save the United States more than \$11 billion by 2050 in avoided impacts. These pre-border efforts are often coupled with the post-border protection efforts of inspection, quarantine, and treatment of imported materials that facilitate interception of insect pests and pathogens prior to their potential escape.

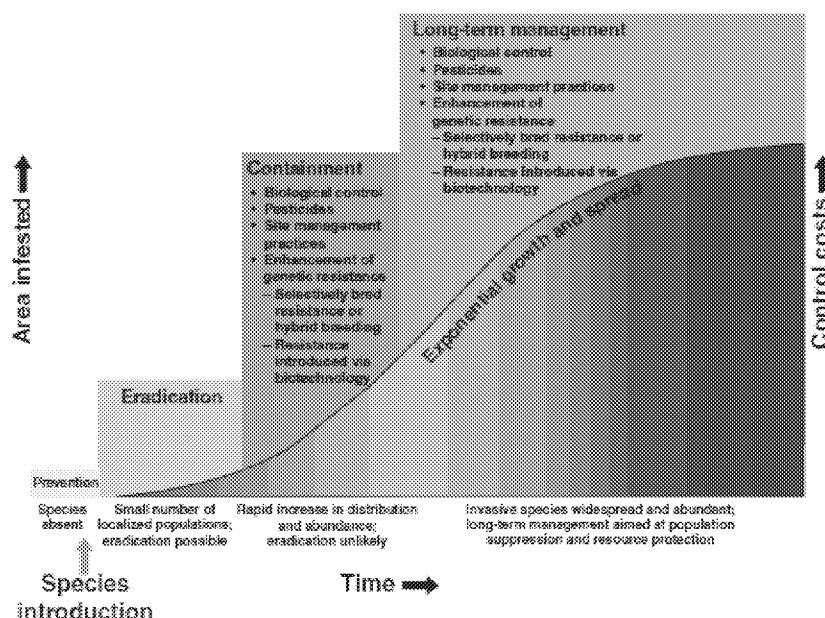


FIGURE 3-1 Stages through time of the typical process, extent of infestation, and control costs associated with the introduction of insect pests and pathogens. SOURCE: Adapted from GAO, 2015.

EARLY DETECTION AND RAPID RESPONSE

Early detection and response programs are essential to prevent the spread of introduced insect pests and pathogens, although these practices may not be effective against microscopic species (i.e., most pathogens) (Liebhold et al., 2016). In addition, public awareness through educational programs may be instrumental in minimizing the entry of harmful organisms and their early detection.

Surveillance methods to facilitate early detection can include deployment of pheromone and other traps, monitoring of sentinel trees or vulnerable sites, and solicitation of reported sightings (Kalaris et al., 2014). Spatial modeling of locations of highest risk of invasion (Venette et al., 2010) can guide deployment of early detection efforts. Liebhold et al. (2016) reviewed both the uses of and methods for surveillance, ranging from baseline early detection to infestation delimitation, to verify the success of an eradication effort.

Eradication

Eradication (see Figure 3-1) is dependent on effective early detection efforts because eradication is more successful when introduced populations cover small areas (Liebhold et al., 2016). Success is also dependent on the detectability of the insect pest involved and whether species-specific control tools are available (Tobin et al., 2014). Chemical traps, mating disruption (e.g., releasing sterile insects), and insecticide fumigations can be used to eradicate small populations of insect pests. For example, pheromone traps have been deployed at the advancing front of the introduced gypsy moth (*Lymantria dispar*) for early detection of spreading populations that can then be treated (Sharov et al., 2002). For pathogens, mechanical removal of the infected host may be the only viable practice, given that detection of the pathogen may not be feasible before infestation. Overall, eradication can either remove or contain the threat or delay the spread of the insect pest or pathogen while more effective management methods are developed (Liebhold et al., 2017).

Although the ability to eradicate pests has improved over time (Liebhold et al., 2016), many attempts have been unsuccessful. For example, eradication of white pine blister rust (*Cronartium ribicola*) to protect species of five-needle pine was a multimillion-dollar effort extending over more than 50 years in the 20th century. The principal approach was through removal of *Ribes* species (e.g., currants and gooseberries), the alternative host for the pathogen to complete its life cycle. However, this effort is regarded as a failure in the western United States (Maloy, 1997). As of 2018, it is generally acknowledged that white pine blister rust will have a permanent presence in North America. Emerald ash borer, first detected in Michigan in 2002, was found in Ohio and Maryland in 2005, indicating that eradication efforts were not effective. Attempts at eradicating the emerald ash borer were unsuccessful in part because of unintentional long-distance dispersal in nursery stock, movement via infested firewood and vehicles, the long-distance dispersal ability of the insect, the difficulty in detecting the early stages of infestation, the absence of a long-range sex or aggregation pheromone, and the lack of a suitable attractant for mating disruption (Mercader et al., 2011, 2016; McCullough and Mercader, 2012). In other instances, eradication efforts have been constrained by negative public reactions to the methods used, such as removal of potential host trees, release of irradiated insects, or broad spraying of a pesticide (Liebhold et al., 2016). Further review of this literature can be found in Liebhold et al. (2016).

CONTAINMENT AND LONG-TERM MANAGEMENT

When eradication of a nonnative is not possible or the spread of a native or established nonnative pest is inevitable, a variety of management options may be pursued. One option is to take no action. Although the option to take no action often is the de facto outcome because the discovery of a new introduction or recognition of increasing impacts of a species already present lags the infestation of hosts (Liebhold et al., 2017), the committee defines “no action” as a deliberate management decision that is weighed against other options. Options to minimize the effects of insect pests and pathogens include (1) biological control,

(2) site management practices (including applying the types of chemical, host removal, and sterile insect techniques also used for eradication), and (3) enhancement of genetic resistance through selective breeding, hybridization, or biotechnology. These options may be implemented independently or in combination.

No Action

The decision to take no action may result from a determination that the insect pest or pathogen is unlikely to have significant (further) impacts on individual species or forest health, a lack of resources, or an inability to identify an effective action to take. This last reason would likely inspire further research if significant impacts are anticipated. The decision to take no action recognizes that vulnerable tree species may decline or be lost entirely, with potential cascading impacts on other species and ecosystem services. The ecological effects will depend on the role of the tree species in the environment, whether replacement species fill similar niches, and whether replacement species are themselves later subject to pest outbreaks. The no-action decision may be made at the time that the host tree is threatened or when restoration (e.g., via breeding or breeding in combination with a biotechnology approach) is considered.

Biological Control and Integrated Pest Management

Biological control is the intentional introduction or application of populations of natural enemies or competitors to control insect pest species (Kenis et al., 2017). Two types of biological control have been effective against introduced insects. The insect pest itself can be manipulated to reduce population growth (e.g., release of sterile males to suppress population growth by competing with fertile males). Alternatively, if the lack of natural enemies (i.e., enemy release) in the new range is the major driver of the outbreak, specialist natural enemies can sometimes be identified in the indigenous range of the introduced insect pest species and released into the area of invasion (Liebhold et al., 2017).

Biological control can be non-self-sustaining, such as when large numbers of sterile males of the insect pests are released, inundating the population sufficiently to dominate breeding, thus reducing the growth of a pest population. In this case, the released organisms are not self-sustaining in the environment, so this approach requires release whenever population control is necessary.

Self-sustaining biological control methods include introduction or augmentation of natural enemies that reproduce and are maintained in that location without successive applications. For North American trees, these include control of species such as the winter moth (*Operophtera brumata*) and the larch case bearer (*Coleophora laricella*) with parasitoid insects introduced from overseas or from another region of the North American continent (Wainhouse, 2005; Kenis et al., 2017). Management practices that favor native predators of the insect pests (conservation biological control), such as providing shelter and alternative food sources for those species, are also common strategies to minimize the likelihood of damage from insect pests (Tscharntke et al., 2007). Overall, a review of biological control in the United States concluded that establishment of biological control agents targeting insect pests of trees has been more successful than those targeting pests of herbaceous species (Kenis et al., 2017); still, the success of these programs can be quite variable (see Box 3-1). Both Liebhold et al. (2017) and Kenis et al. (2017) provide reviews of biological control efforts to reduce the impacts of insect pests on trees.

Hypovirulence is a biological control strategy for mitigating or suppressing the effects of some fungal pathogens. Some viruses can infect pathogenic fungi, reducing their ability to infect, colonize, kill, and reproduce on susceptible hosts (Boland, 2004). If these viruses are spread in the area infested with a problematic pathogen, in some instances they may reduce the virulence of the pathogen of interest. Success with this strategy has been demonstrated in Europe on strains of Dutch elm disease (Boland, 2004) and chestnut blight (see Box 3-1; Grente and Sauret, 1969; Grente and Berthelay-Sauret, 1978).

BOX 3-1 Biological Control Efforts and Site Management Practices in Case Study Species

American Chestnut

As mentioned in Chapter 2, site management practices such as chemical treatments and clearing and burning were ineffective in controlling chestnut blight in the early 20th century (Stoddard and Moss, 1913). Biological control via hypovirulence, however, shows some potential because the European chestnut (*Castanea sativa*) also suffered severe damage from the chestnut blight fungus in the early 20th century but recovered substantially due to the emergence and deployment of hypovirulent strains of the fungus (Grente and Sauret, 1969; Grente and Berthelay-Sauret, 1978). Trees infected with *Cryphonectria parasitica*, which in turn are infected with the hypovirus, show restricted canker development and are able to continue growing and reach maturity (Jacobs et al., 2012).

In contrast to the results in Europe, however, the hypovirulent fungal strains in North America have limited ability to spread from tree to tree and spread much more slowly than the uninfected fungus; therefore, American chestnut populations are not protected (Anagnostakis and Hillman, 1992; Milgroom and Cortesi, 2004). The spread of the hypovirus depends on fusion (anastomosis) of the hyphal filaments (mycelia) that constitute the vegetative growth of the fungus. The vegetative structure formed by the hyphae is known as the mycelium. The failure of the hypovirus has been attributed to multiple genetic variants of the “wild type” fungi that express different vegetative incompatibility (*vic*) genes. If the *vic* genes match, fusion of hyphae may occur. If the *vic* genes do not match, fusion of hyphae is blocked and the hypovirus is not transferred. Therefore, the spread of hypovirulence from tree to tree is blocked by mycelial incompatibility (Liu and Milgroom, 1996; Milgroom and Cortesi, 2004). It is assumed that there are a larger number of mycelial incompatibility groups in North American fungal populations than in Europe (Liu et al., 2002).

Genetic analysis has identified six diallelic *vic* loci (loci with two alternative *vic* alleles) regulating vegetative incompatibility (Cortesi and Milgroom, 1998). These genes have been identified at the molecular level (Choi et al., 2012) and have been disrupted using an adapted *Cre-loxP* recombination system resulting in the loss of the incompatibility barriers. The results demonstrate the feasibility of a “super” hypovirus that could overcome the genetic incompatibilities and transmit a virulence-attenuating hypovirus for biocontrol of the chestnut blight fungus (Zhang et al., 2014; Zhang and Nuss, 2016). Hypovirulence may yet become useful in combination with host resistance for biocontrol of blight (Griffin, 2000).

Whitebark Pine

A limited number of studies have used fire or fire-surrogate treatments (thinning, fuels enhancement, or small selective cuts to encourage nutcracker caching) to investigate efficacy at increasing regeneration of whitebark pine. High- and moderate-intensity prescribed fire treatments along with selective cutting combination treatments were successful in creating nutcracker caching habitat; however, few to no whitebark pine seedlings had established after 5 years (Keane and Parson, 2010). This lack of regeneration, even when nutcracker caching was high, may be due to many factors, and the assessment time frame may have been too short to detect effects because whitebark pine may take decades to reestablish (Arno and Hoff, 1990; Tomback et al., 2001). It may also be possible that, in areas where high mortality of cone-bearing trees has occurred, nutcrackers recover most seed caches for food, leaving few to no seeds to germinate (McKinney and Tomback, 2007).

Furthermore, studies have revealed that prescribed fire often kills many mature whitebark pines while the numbers of competing subalpine fir targeted for removal remain higher than desired (Keane and Parsons, 2010). Some fire treatments also increase ground fuel loads by causing blister rust-killed snags to fall, although such downed wood may be beneficial to whitebark pine regeneration by providing shelter supporting the establishment of seedlings (Keane and Parsons, 2010). In any case, returning fire to fire-suppressed whitebark pine forests is not simple, and its efficacy in restoration remains unknown.

(Continued)

BOX 3-1 Continued**Ash**

Containment and management strategies related to emerald ash borer (EAB) have focused on prevention of further dispersal and diminishing insect pressure through insecticides and biological control (Poland and McCullough, 2006). Evaluation of the effectiveness of EAB containment strategies (selective removals, quarantine, and insecticide treatments) has shown that they fail to prevent the dispersal of EAB (Mercader et al., 2011, 2016; McCullough and Mercader, 2012). Selective removal does not prevent dispersal once infestation is detected in a given tree because EAB has already dispersed to uninfested hosts. Quarantines have also proven quite disappointing for preventing dispersal, partially for the same reason that selective removals are ineffective because of human agency. While quarantines slowed the movement of infested nursery stock and dispersal, the movement of infested saw logs and firewood continued. EAB hitchhiking on vehicles and trains has been documented in the United States and in Russia where green ash is widely planted as a street tree. Hitchhiking, rather than transport of infested wood, may be a major dispersal method between widely separated cities along the interstate highways in the United States (Prasad et al., 2010); this may explain the appearance of EAB in Boulder, Colorado, in 2016, more than 880 km distant from the nearest infestation in Omaha, Nebraska. With regard to insecticide treatments, no naturally occurring microbial insecticide (e.g., *Bacillus thuringiensis*) has proven effective in killing adult beetles via aerial application or in a forest setting (McCullough et al., 2015).

Biocontrol efforts targeting EAB started in 2007 in Michigan. Researchers released three EAB parasitoid species from China, the egg parasitoid *Oobius agrili*, the larval endoparasitoid *Tetrastichus planipennisi*, and the larval ectoparasitoid *Spathius agrili* (*Federal Register*, 2007; Bauer et al., 2015). *T. planipennisi* can effectively control EAB attacking ash saplings and young stump sprouts (Duan et al., 2017). Once the tree develops thick bark, the ovipositor is too short to reach the EAB larvae (Abell et al., 2012; Duan et al., 2017). Although studies show successful establishment of these parasitoids in some areas, the range of *S. agrili* (Hymenoptera: Braconidae) is limited by its lack of cold tolerance (Duan et al., 2012). Other parasitoids (e.g., *S. galinae*) had been approved for release as of 2018; they were expected to perform well in colder climates and have ovipositors that can penetrate the thicker bark of older trees (Belokobylskij et al., 2012; Duan et al., 2014). Long-term monitoring years after the release and establishment of one or more of the introduced parasitoids reveals that EAB still persists after ash population collapse, maintaining very low population levels on ash saplings as small as 2 cm in stem diameter (Aubin et al., 2015).

Poplar

Several chemical control methods have been developed that are effective against *S. musiva*, including repeated application of the fungicide benomyl to control the spread of cankers in the field (Ostry, 1987; Liang et al., 2014). Various biological control mechanisms using bacteria (Gyenis et al., 2003) and fungi (Yang et al., 1994) have also shown some success in controlling *S. musiva*. These practices may help inhibit the spread of *S. musiva* in nursery operations, but the extent and frequency of treatment required makes them impractical in operational plantations (Ostry, 1987) or in wild populations.

Site Management Practices

Whether to contain a pest from spreading or as a strategy for long-term management, there are a number of site management practices that create conditions unconducive to a pest outbreak. Use of chemicals, such as pesticides and fungicides, are common practices in managed forests. However, reliance on chemical controls is generally not a long-term solution because of the long-recognized potential consequences of widespread pesticide use. These consequences may include evolution of resistance in the pest, nontarget impacts, substantial expense associated with repeated treatments, and public opposition to widespread use of potential toxins (Mack et al., 2000; Gould et al., 2018).

As in eradication efforts, quarantines may be put in place to prevent the movement of contaminated wood, and infested or infected trees may be removed. For example, when the Asian longhorned beetle (*Anoplophora glabripennis*) was discovered infesting multiple tree species in urban parks and suburban neighborhoods (Haack et al., 2010) in New York in 1996 and in Chicago in 1998, survey, chipping and burning of infested trees, and quarantined movement of potential host species (including nursery stock) were all rapidly implemented. Uninfested host trees within specific distances from infested trees were treated with insecticide. However, despite successful eradication in several sites, repeated introductions of the beetle means that it remains a threat to U.S. forests (Haack et al., 2010). With regard to emerald ash borer (EAB), tree removal, quarantine, and insecticides have not been effective (see Box 3-1).

Another site management practice to minimize the conditions that favor the onset of an outbreak is thinning. Silvicultural thinning of managed stands is often conducted to improve growth; this practice also promotes individual vigor, increasing tree defenses against insect pests and pathogens (Gottschalk, 1993; Maher et al., 2018). For example, mountain pine beetle (*Dendroctonus ponderosae*) is one of the native insect pest species predicted to expand its distributional range under climate change (Raffa et al., 2013). Outbreaks of this species are driven by drought and even-aged stands of mature trees. In this situation, thinning stands and removing infested trees may reduce the beetle population below the outbreak threshold. Thinning of the understory also removes fuel for wildfire, reducing the probability of tree mortality.

Pruning, rather than thinning, can also be an option in silvicultural stands. For example, branch pruning of white pines can reduce the impact of white pine blister rust (Ostry et al., 2010; Schwandt et al., 2010). This approach is feasible only where white pine species are in silvicultural management. Pruning focuses on protecting existing trees and their genetic diversity but does not increase the genetic resistance of future progeny.

Maintaining diverse forests and planting mixed stands where the site naturally supported multiple species is another management tool to promote ecosystem resistance to insect pests and pathogens. More diverse forests are subject to lower levels of herbivory by insects than are more homogeneous forests, and this effect increases with the taxonomic distances among trees and with the proportion of unaffected species (Jactel and Brockerhoff, 2007). This phenomenon is due to the dilution effect of the host species, which reduces both population growth and spread of the insect when the host tree is not abundant (Keesing et al., 2006, 2010). However, the dilution effect may not be as strong when generalist species (those that make use of multiple tree species) are involved (Jactel and Brockerhoff, 2007). A similar dynamic is hypothesized for disease transmission, which can be diluted with a decrease in abundance of the host species. Even in the case of generalist pathogens, such as *Phytophthora ramorum*, a decrease in virulence has been observed under diverse host conditions (Haas et al., 2011). Furthermore, diverse forests will likely experience lower stress from climate change–related drought because diverse stands have higher productivity and resilience to drought than monospecific and low-diversity stands (Rasche et al., 2013). In this case, reduced intraspecific competition and niche partitioning for resources such as nutrients, light, and water are likely the causes. Where forests are naturally less diverse, with one or two predominant species, options other than managing for overstory diversity will likely be more effective and appropriate.

Breeding to Enhance Resistance

Plants that are tolerant of insect pests and pathogens maintain productivity despite the presence of the damaging species. Plants that are genetically resistant maintain productivity by reducing the ability of the insects and pathogens to establish and cause stress (Leimu and Koricheva, 2006). Both tolerant and resistant plants have characteristics that allow persistence and growth despite the presence of damaging insects and pathogens and may be used in breeding programs designed to reduce vulnerability of tree populations (Snieszko and Koch, 2017; Woodcock et al., 2017). In this report, the committee uses the term resistance to include tolerance, as the two responses cannot always be easily distinguished in the field without further research.

Genetic resistance confers lack of or reduced susceptibility to an array of threats, including insects and diseases (Telford et al., 2015; Sniezko and Koch, 2017; Woodcock et al., 2017; Showalter et al., 2018). The nonnative insect pest or pathogen may cause high mortality in the affected species in the forest, but genetic variation often allows some individuals to survive. Many forest tree species have at least some genetic resistance, even if at low frequencies, to most pathogens or insects (see Box 3-2; Lattanzio et al., 2006; Sniezko and Koch, 2017; Woodcock et al., 2017).

The first priority in selective resistance breeding is to answer the following questions:

1. Is there genetic resistance in the host tree, and if so, what type and degree of resistance exists within a tree and its progenies?
2. What is the geographical distribution of trees having resistant phenotypes?
3. What is the frequency of the resistant phenotypes within host tree populations?

Finding suitable parent trees can be difficult. Additionally, finding resistant parent trees does not mean all of the progeny from the parent trees will be resistant (Sniezko et al., 2014; Sniezko and Koch, 2017) and restoration plantings need to account for this. Resistance is a phenotype that usually results from a complex interaction of multiple genes across a multiplicity of environments. The simple, one-gene, Mendelian, dominant pest resistance cases occupy much of the literature because such systems are tractable and can be studied within the time and funding limits imposed on academic research. However, as in crop species, in many cases this form of resistance may not be durable in forest trees (McDonald and Linde, 2002; Kinloch et al., 2004; Palloix et al., 2009); rather, durable resistance may only be possible with polygenic genetic mechanisms (see American chestnut case in Box 3-2). Evaluating the durability of resistance within individuals and across generations (Mundt, 2014; Sniezko and Koch, 2017) will also be paramount because trees will be on the landscape for decades to centuries. Effectively applying selective-breeding programs requires that these rare cases of resistance be identified and propagated in greenhouses or seed orchards and intercrossed to generate progeny with polygenic resistance for deployment in restoration and reforestation programs (Sniezko and Koch, 2017; Woodcock et al., 2017).

In the case of nonnative pathogens or insects, a greater understanding of controls on pest population dynamics in the home range of the pathogen or insect would provide a valuable perspective on what type of resistance might have a high likelihood of success. For example, in Asia, what resistance is present in the native white pine species, where presumably the pines and the white pine blister rust fungus have co-evolved? It would be helpful to know if similar resistance exists (at even low frequency) in North American white pines. In addition, in some areas of Asia, white pine blister rust has become problematic (La, 2009; Zhang et al., 2010). Knowing the cause of that change—perhaps due to new land management practices, evolution of greater virulence in the rust, or changing climate—would also be useful information. Further study from a global perspective to understand coevolved systems and how they can be disrupted will help design strategies to restore species (including how to use any biotech option) and help refine models to increase understanding of the potential long-term efficacy of resistance and its impacts over the landscape.

Another way to introduce genetic resistance into a susceptible tree species is to hybridize the susceptible species with a related resistant tree species. After hybridization, the offspring are backcrossed with different trees of the susceptible tree species to maintain genetic diversity. In theory, repeated backcrossing will result in resistant trees with genomes that are almost entirely consistent with those of the susceptible parent species, with the exception of the regions containing alleles that confer resistance to the insect pest or pathogen (Woodcock et al., 2017). In practice, this result is rarely achieved without intensive monitoring with DNA markers and large backcross population sizes. Backcross breeding is most effective for introgression of resistance when resistance is due to one or two dominant factors. Even in the simple case of only one or two factors, if one or both of these factors are recessive, the breeding strategy must include selfing or intercrossing alternating with backcrossing. Backcross breeding strategies may be greatly accelerated using marker-aided selection or genomic selection, particularly when the goal is to capture multiple resistance factors from the nonnative species. A good example of a backcross breeding program is the one undertaken to introduce blight resistance into the American chestnut from the Chinese chestnut (see Box 3-2).

BOX 3-2 Progress in Resistance Breeding in Case Study Species*American Chestnut*

Initial attempts to breed chestnut with resistance to chestnut blight began in the 1920s but ended unsuccessfully in the 1960s (Steiner et al., 2017). A renewed effort began in earnest in the 1980s with the formation of The American Chestnut Foundation (TACF) and the American Chestnut Cooperators' Foundation (ACCF) (Griffin et al., 2006). The ACCF has used breeding within the *C. dentata* species to complement use of hypovirulence (Jacobs et al., 2012). TACF pursued a hybrid and backcross method to incorporate resistance from the Chinese chestnut (*Castanea mollissima*) into the American chestnut (see Figure 3-2). This approach was initiated after it became clear that relatively little genetic resistance exists in native populations of American chestnut. The Chinese chestnut has, on average, moderate to good resistance to the blight fungus, but individual trees may have some susceptibility (Huang et al., 1996). Early crosses of the Chinese chestnut to the American chestnut showed that some F₁ hybrids were resistant (Burnham, 1988; Anagnostakis, 2012). Based on this observation, it was assumed that the resistant hybrid phenotype was due to a small number of dominant genes. If that were true, then repeatedly backcrossing the hybrids to American chestnuts and selecting for resistance would ultimately result in a resistant chestnut with a high-percent of American chestnut ancestry. After several cycles of backcrossing, the resistant progeny populations could be intercrossed and selection continued for resistance as well as other American chestnut traits such as tree form and rapid growth. In this way, genotypes that were essentially American chestnut in phenotype but carried resistance to blight could be created.

As of 2018, this program was still ongoing, with an objective of imparting the resistance from the Chinese chestnut while trying to capture the growth, adaptability, and other characteristics of the American chestnut. However, the degree of resistance from selection has been disappointing after over 30 years of backcrossing and intercrossing for a number of reasons, including the difficulty of phenotype evaluation and the resulting lack of information on the underlying genetic architecture of resistance.

The first releases from TACF intercrossed populations in 2007 had American chestnut growth rate and form for the most part, but the degree of blight resistance needed for sustainable survival in natural forest areas had not yet been achieved as of the time the committee was writing its report (Steiner et al., 2017). The most advanced backcross hybrids are descendants of a small number of hybrids of American and Chinese chestnuts, particularly the Clapper hybrid (Clapper, 1963), the Graves hybrid (Graves, 1942) and a third hybrid, "Nanking" (Diller et al., 1964). More than 17,000 descendants of these hybrids have been tested for resistance, site adaptation, growth, and form (Sisco, 2004; Hebard, 2006). Seed orchards have been established in Virginia and Pennsylvania to increase numbers of nuts needed to implement large-scale forest trials. A continuing strategy includes retaining only those trees with sufficient blight resistance and a timber-type growth form. Genomic selection, a strategy based on the association of phenotypic performance with genome-wide patterns of DNA polymorphisms, is also in progress.

Blight-resistant chestnuts reintroduced in southern Appalachian regions will also need to have resistance to *Phytophthora cinnamomi*, the agent of ink disease. Recent work has demonstrated resistance in TACF populations descended from Chinese and American chestnuts and in some of the hybrid progeny of the European chestnut (*C. sativa*) by the Japanese chestnut (*C. crenata*) (Santos et al., 2015; Westbrook et al., 2018). At the time the committee wrote its report, resistance screening of young seedlings was under way and showed promise (Jeffers et al., 2012; Steiner et al., 2017) and could be combined in the future with blight resistance through breeding (Steiner et al., 2017).

Whitebark Pine

A selective breeding program for whitebark pine with resistance to white pine blister rust has been ongoing since the 1990s in the Oregon and Washington portions of the species' range. Cones are collected from candidate parents identified in the field, and seedlings grown from those cones are infected with the disease at about age 2 or 3 using an inoculation system previously developed to identify resistance in other white pine species (see Figure 3-3). Seedling families are assessed for up to 5 years for the type and degree of resistance, and this information is used to rate the parent's resistance (Snieszko et al., 2011, 2018).

(Continued)

BOX 3-2 Continued

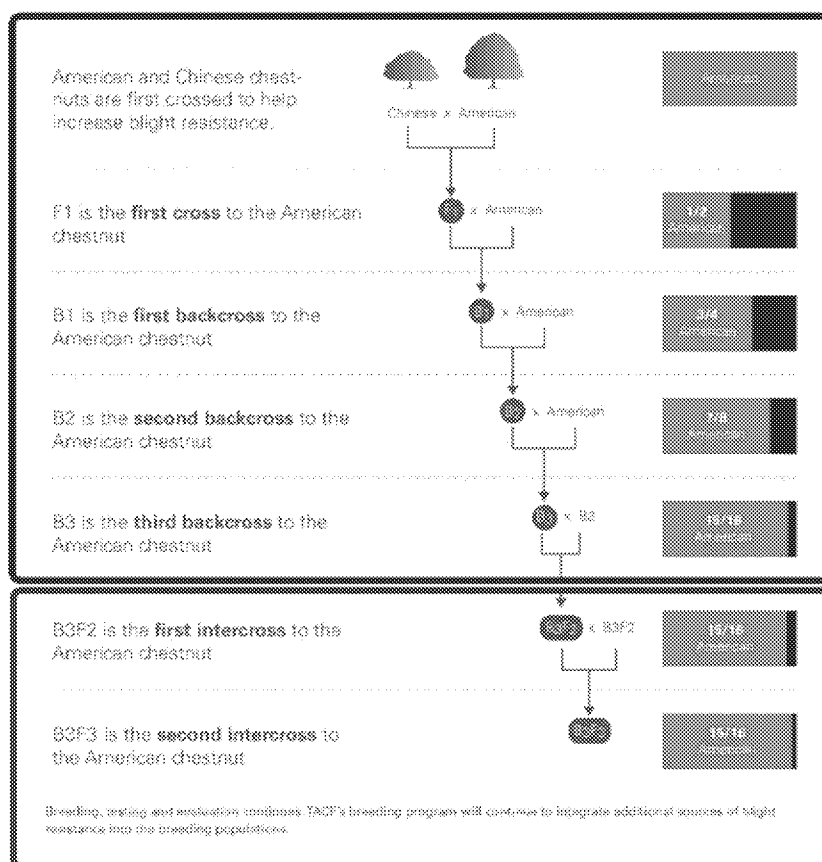


FIGURE 3-2 Overview of the theoretical expectations upon which the American Chestnut Foundation backcross breeding program was initially based. NOTE: The illustrated “recovery” of the native American chestnut with each round of backcrossing is based on theoretical expectations that are rarely achieved in practice unless DNA marker-assisted selection is used in every generation. SOURCE: Westbrook, 2017.

The first seedling inoculation trials started in 2002; additional trials have been undertaken when seed from new parent tree selections becomes available. Through 2018, the progeny of 1,225 parent trees had been tested for rust resistance for the nine seed zones in Oregon and Washington. Of these 1,225 parent trees, preliminary resistance ratings were available for 1,002 trees. The data from the seedling trials suggest that 394 of these trees have levels of resistance that may be useful in restoration efforts. However, the frequency of resistance varies geographically (e.g., by breeding zone or management unit, see Figure 3-4), which adds logistical complications to the resistance discovery and deployment process. In one of these zones, only 2 of 28 tested parent trees have even marginally useable degrees of resistance, while in another seed zone, 93 of 106 trees have useable degrees of resistance. The degree of resistance in some populations of whitebark pine in the Oregon and Washington portions of the species range is high enough that land managers can collect seed from the highly rated parent trees to use immediately in restoration, without waiting the decade or more to establish orchards, then produce and distribute seed.

(Continued)

BOX 3-2 Continued

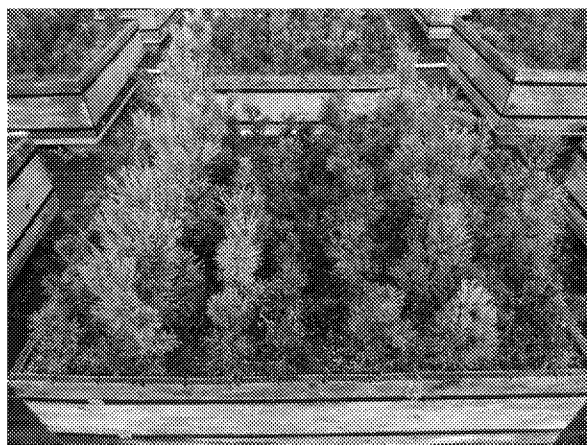


FIGURE 3-3 Testing whitebark pine for resistance to white pine blister rust at USDA Forest Service's Dorena Genetic Resource Center. NOTES: Two-year old seedling progeny of different parent trees are inoculated with the pathogen and evaluated for up to 5 years. Note the large difference in survival among seedling families (each in a separate 10-tree row plot); for example, in the far left row all seedlings from one parent tree are dead or dying (red) whereas the next row to the right has seedlings from another parent tree that are alive (green). SOURCE: R. Sniezko.

Resistance breeding programs for white pine blister rust are also under way in the interior western part of the species range and in western Canada (Sniezko et al., 2011, 2018). This concerted effort will provide a good genetic base of resistant trees, permitting a restoration effort for each seed zone that initially contains a minimum number of resistant parent trees. The mechanism of resistance is still not well understood, but progeny tests suggest that the trait is polygenic, as is the case in other species of white pine (Kinloch and Dupper, 2002). Field trials (under way at the time the committee wrote its report) will more fully define the level of expected survival in resistant progeny in areas of varying rust hazard and environmental conditions. So, at least for whitebark pine (in at least some seed zones), selective breeding offers an efficient method to develop resistant seedlings for restoration. The restoration plantings will need to be followed to examine durability of the genetic resistance in whitebark pine as well as stability of resistance in different environments.

One of the challenges of using native resistance is the need to protect the resistant parent trees from other sources of mortality while the next generation of seed trees is maturing. A number of the blister rust-resistant parents have already been lost to fires or to attack by mountain pine beetle (*Dendroctonus ponderosae*). The semiochemical verbenone (an antiaggregation pheromone) has been used to protect individual trees from mountain pine beetle attacks (Perkins et al., 2015) and can be particularly useful to protect the resistant parent trees used for seed collections for the future restoration efforts. Verbenone is not 100 percent effective, and it needs to be applied each year as conditions warrant. Other chemicals, carbaryl and pyrethroid insecticides have also been registered to help protect trees from mountain pine beetle (Hastings et al., 2001; Fettig et al., 2013).

As with white pine blister rust, genetic resistance to mountain pine beetle has been found (Six et al., 2018). Resistance of pine species to outbreaks of mountain pine bark beetle depends upon several factors including resin responses and secondary chemistry (Huber et al., 2004; Franceschi et al., 2005; Raffa et al., 2008). These resistance factors are generalized against many insects and pathogens, but natural selection has likely shaped their form and strength in forests that have experienced strong bark beetle pressure over millennia. However, Raffa et al. (2013) have indicated that the "typical" mechanisms of resistance to mountain pine beetle found in lodgepole and ponderosa pine (high resin production and induced defenses) are poorly developed in whitebark pine. This circumstance might be expected for a naïve host tree that has not had strong evolutionary pressure to develop costly defenses (Cudmore et al., 2010). Indeed, the lower overall resistance of naïve hosts that have had little to no exposure to bark beetle—including lodgepole and jack pine in areas where the beetle is expanding its populations (northern British Columbia and Alberta) and high-elevation whitebark pine—has been well documented (Cudmore et al., 2010; Raffa et al., 2013; Bentz et al., 2015).

(Continued)

BOX 3-2 Continued

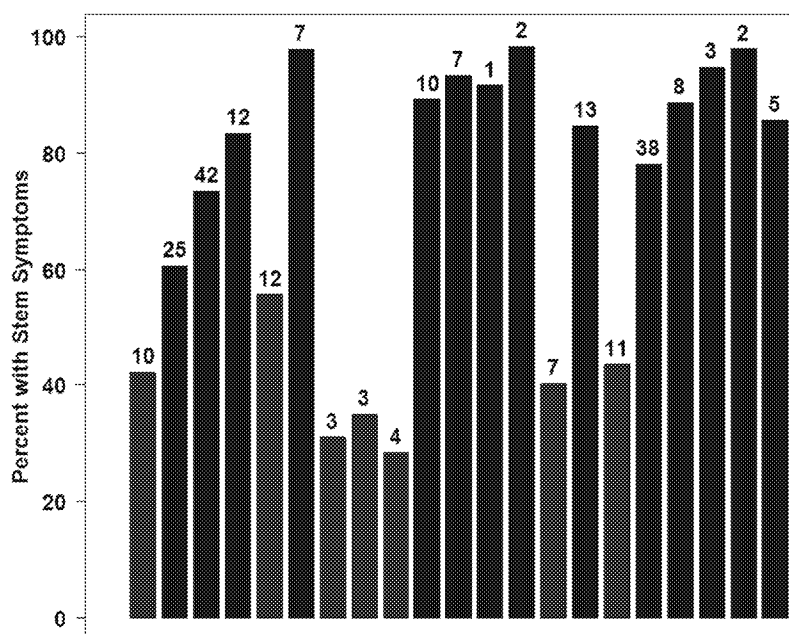


FIGURE 3-4 Variation in genetic resistance (percent of seedlings with stem symptoms ~15 months after inoculation) to white pine blister rust in whitebark pine among different geographic populations from throughout the range of the species from a seedling inoculation trial initiated in 2007 at Dorena Genetic Resource Center. NOTES: The number of parents tested using half-sib families in each seed source mean is indicated above the bar. The 18 Oregon and Washington sources (first 18 bars from the left) represent individual National Forest, National Park, and Confederated Tribes of Warm Springs boundaries from which the seedlots were collected. The right-most three bars refer to seedlots from California, Idaho, Montana, and British Columbia. Populations range from highly susceptible (blue, >60% of the progeny showing early stem symptoms) to moderately resistant (red, families showing <60% of the progeny with early stem symptoms). SOURCE: Snieszko et al., 2018.

Likewise, the conventional wisdom that asserts that faster growing pines are more resistant to bark beetle may not hold with whitebark pine. In past outbreaks, whitebark pines that survived were slower growing than those that were killed (Margoles, 2011). This slow growth, along with evidence that whitebark pine may not have the capacity to produce strong defensive responses even when healthy (Raffa et al., 2013), indicates that prescriptive thinning to release the host from competition may fail to reduce mortality.

However, resistance may still prove to be a powerful tool, although it may take a different form. Strong resistance to bark beetle has been described wherein trees escape attack, not through the production of strong resin or chemical defenses, but rather the opposite: by producing greatly reduced chemical profiles that interfere with beetle recognition or attraction to hosts. Mature whitebark pine surviving a recent outbreak have been found to be genetically distinct from beetle-susceptible trees (Six et al., 2018). Whether the putative genetic resistance to mountain pine beetle proves to be durable is uncertain (as is resistance to blister rust) and will need further study and confirmation from the field over time. Natural selection may be acting quickly to enhance adaptation to changing conditions. High selection pressure that results in strong natural selection for beetle resistance and drought tolerance would be particularly valuable in the vast inaccessible areas of whitebark pine's range that not are amenable to active restoration.

The same challenges exist in breeding and outplanting trees resistant to bark beetle as exist for resistance to blister rust, given whitebark pine's long maturation period. Also, whitebark pine with resistance to blister rust remains susceptible to beetles, and whitebark pines with beetle resistance are typically susceptible to blister rust. An integrated approach will be needed to look for correlates of resistance to the two threats to include in breeding programs for the restoration of this tree.

(Continued)

BOX 3-2 Continued

Ash

All of the ash species native to North America have some susceptibility to the EAB, with the widely distributed green ash and white ash being very susceptible. Monitoring forests for individual trees with intact canopies after most of the ash in the monitored plot have died from EAB was initiated a few years after EAB was detected in Michigan in 2002 (Knight et al., 2012). A small number of green and white ash trees (<1 percent) survive EAB attack many years longer than conspecifics in the same stand. These “lingering ash” show evidence of less severe EAB infestation, often accompanied by vigorous wound healing, and maintain a healthy crown for years after local conspecifics have died (Knight et al., 2012, 2013; Koch et al., 2015). Replicated studies reveal reproducible quantitative differences in defensive responses to EAB larvae between lingering ash and susceptible ash genotypes (Koch et al., 2015). Crosses between two lingering ash parents produce progeny with greater larval-killing response than either parent (see Figure 3-5). This result suggests that the parents have different partial resistance responses that have a genetic basis. These progeny can form the basis of a breeding program for “stacking” or pyramiding the allelic variants at multiple loci that may be responsible for the variety of partial-resistance phenotypes.

Alternatively, the best progeny can be grafted and planted in seed orchards to enable natural intercrossing for the production of seed for restoration efforts. This approach requires a monitoring, breeding, and phenotyping program. Monitoring is needed to identify more lingering ash from different areas of adaptation, to maintain genetic diversity. Breeding is needed to stack up the genetic factors that contribute to the resistance phenotypes. Finally, continued phenotypic screening of grafted clones and progeny of newly identified lingering ash verifies that the resistance phenotypes have a genetic basis. The advantage of the selective breeding approach, in this case, is that the basis of the resistance is polygenic. Plant pests and pathogens do not overcome polygenic resistance, as quickly as monogenic resistance (Parlevliet and Zadoks, 1977; Carson and Carson, 1989; Simmonds, 1991; Tuzun, 2001; Mundt, 2014). The work on finding additional resistant ash selections continues, as does the breeding. Field tests will be needed to determine the efficacy and durability of the resistance from the selective-breeding programs. The time line for restoration with genetically resistant ash will depend on the search for additional selections and the results in the field trials.

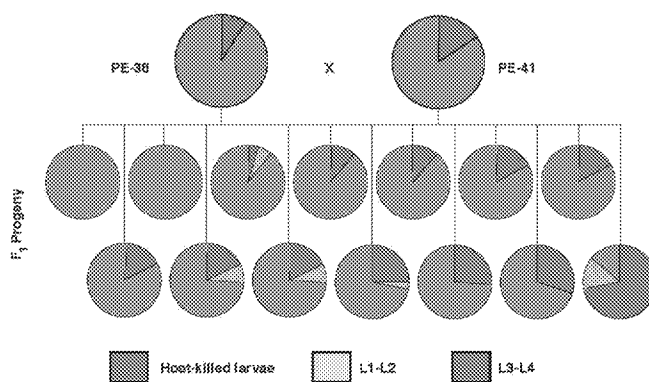


FIGURE 3-5 Larval-killing response in the F₁ progeny of two lingering ash parents. NOTES: Pies indicate responses of the parents (PE-L38 and PE-L41) and of individual progeny. Colors indicate, by tree, the proportion of host-killed larvae (brown), early instar larvae (L1-L2, green), and late instar larvae (L3-L4, blue) 8 weeks after egg application. Parent evaluation was done in replicated tests in previous years. SOURCE: Jennifer Koch, unpublished data.

Backcross breeding to closely related resistant species is not an option for most of the North American *Fraxinus*, because these species are genetically incompatible with the Asian *Fraxinus* species that exhibit resistance to EAB. Black ash, a very susceptible North American riparian species, is compatible with the more resistant Asian *Fraxinus*, but a selective-breeding program, while possible, had not been undertaken as of 2018. If such a program did exist, then the use of transcriptome-based markers to identify quantitative trait loci regions would be feasible, because the whole genome sequence and deep transcriptome sequencing resources exist for *Fraxinus* species (Lane et al., 2016; Sollars et al., 2017).

(Continued)

BOX 3-2 Continued*Poplar*

There have been numerous studies on the genetics of susceptibility and resistance of *Populus* species and hybrids to *Sphaerulina musiva* infection. An early study with a controlled cross suggested that eastern cottonwood (*P. deltoides*) carries a recessive allele that confers resistance and that interspecific hybrids between eastern cottonwood and black cottonwood (*P. trichocarpa*) show intermediate resistance (Newcombe and Ostry, 2001). Similarly, a survey using a greenhouse assay of wild accessions collected in a hybrid zone in Alberta showed that susceptibility to stem cankers was highest in balsam poplar (*P. balsamifera*), lowest in eastern cottonwood, and intermediate in hybrids (LeBoldus et al., 2013). Furthermore, there was minimal interaction between host genotype and fungal strain in susceptibility of hybrid cultivars, suggesting that resistance mechanisms could be enhanced by breeding (LeBoldus et al., 2009). Based on microscopic observations of stem infections, it appears that one of the main mechanisms of canker resistance is the formation of necrophylactic periderm around the point of entry, inhibiting spread of the fungus (Qin and LeBoldus, 2014). Interestingly, because the fungus has necrotrophic characteristics, resistance mechanisms do not involve a typical hypersensitive response, whereby the host limits fungal spread through coordinated cell death around the point of infection. On the contrary, if the hypersensitive response is activated by the infection, this can actually enhance susceptibility to the fungus (Liang et al., 2014; Qin and LeBoldus, 2014). There is also some evidence that the chemical composition of the leaf cuticle can inhibit infection by *S. musiva* (Gonzales-Vigil et al., 2017). Furthermore, leaf and stem infection can be enhanced by stressful conditions such as ozone exposure (Woodbury et al., 1994) or drought (Maxwell et al., 1997).

Using Biotechnology to Enhance Resistance

Another way to generate resistant trees is through the use of biotechnology. Biotechnological research to introduce or modify traits in trees has been explored in a wide range of economically and ecologically important tree species throughout the world. Appendix C contains reports on biotech tree species at all stages of research and development from 1987 through 2018. Often the reports cover establishment of initial proof-of-concept transformation and regeneration systems, which demonstrate bacterial resistance genes from donor species. In species where this system is robust, the appendix includes reports demonstrating the incorporation of genes conferring various traits in the target species. These traits include insect and fungal resistance, early flowering, phytoremediation, tolerance to metal toxicity, herbicide tolerance, improvement of wood quality, changes to lignin content, and tolerance to drought, frost, and salt. The primary approach used has been transgenesis via *Agrobacterium tumefaciens*; however, the table includes reports describing biotechnological approaches such as RNA interference (RNAi) and clustered regularly interspaced short palindromic repeat (CRISPR) (see Box 3-3). For a more comprehensive treatment of the developments in the field of tree biotechnology, see Chang et al. (2018).

The first application for a field test of a biotech tree in the United States was submitted to USDA in 1989 for a poplar modified for glyphosate tolerance (Fillatti et al., 1987). As of 2018, about 700 permits have been issued by USDA-APHIS. However, only two tree species modified using biotechnology had been grown outside of field trials in the United States in that time.¹ The first tree species to reach this stage was papaya (*Carica papaya*). Varieties with resistance to papaya ring spot virus incorporated via transgenesis have been grown in Hawaiian orchards since 1998. The second was apple (*Malus × domestica*) in which RNAi has been used to suppress the expression of polyphenol oxidase genes, resulting in fruit flesh that does not brown when peeled or cut. Nonbrowning apples became available to U.S. consumers in 2017.

¹A variety of plum has been modified via *Agrobacterium*-mediated transgenesis to have resistance to plum pox virus, and this variety has met U.S. government regulatory requirements. However, it is not grown commercially as of 2018.

BOX 3-3 Biotechnological Approaches

Humans have been directly modifying DNA since 1973 (Cohen et al., 1973), and continuous technological advances have improved the efficiency and precision of biotechnology. More than four decades later, there are many biotechnology tools available to manipulate the DNA of almost any organism, including trees. The following is a brief description of the most commonly used approaches.

Mutagenesis

Although the frequency of naturally occurring gene sequence polymorphisms is high in most forest trees, methods have been developed for increasing variation by inducing mutations in the DNA sequence (direct mutagenesis). Many kinds of specific gene mutations have been induced in genes of forest trees. Mutations have been produced to knock out gene activity (loss-of-function mutations). Gain-of-function mutations can be produced through enhanced expression of specific genes. Partial reduction of specific gene function can also be induced by reducing the expression of the target gene (knock-down mutations).

The technology for inducing mutations is diverse. Chemical mutagenesis^a (Riyal, 2011) uses compounds such as ethyl methane sulfonate (EMS) to induce small mutations in DNA sequences. For example, Zayed et al. (2014) used EMS to induce mutations in the tropical tree species kelampayan (*Neolamarckia cadamba*) and petai belalang (*Leucaena leucocephala*) because they determined that these species have a relatively low genetic diversity. Chemical mutagenesis (EMS) of pollen from willow (*Salix* spp.) was shown to create new sequence variants, detected by high-throughput sequencing (Riyal, 2011).

Plants frequently undergo somatic mutations, and these can generate novel genetic variation within a single individual. This kind of mutation is particularly important for trees with long lifespans such as oaks (Plomion et al., 2018) and clonal organisms such as aspen trees (Ally et al., 2010). These mutations can sometimes be adaptive and potentially useful for breeding, as in the case of a mutation in *Eucalyptus melliodora* that enhances resistance to herbivory in branches harboring the mutation (Padovan et al., 2013). Such mutations can be captured in breeding programs (if they enter the germ line) or propagated through rooted cuttings or by stem grafting to rapidly deploy resistance genes.

Transgenesis

Transgenesis involves inserting foreign genes or DNA fragments into cells of a target species to create a new gene sequence. The DNA sequence may be inserted into a target cell through a variety of techniques:

1. Biolistics is a technique that inserts DNA into plant cells by physical bombardment. Tiny metal beads coated with DNA are propelled at high velocity through the plant cell wall into the cells (Klein et al., 1987; Sanford et al., 1987).
2. Electric shock (electroporation) opens plant cell membranes, allowing DNA to enter cells (Fromm et al., 1985).
3. Microinjection (Neuhaus and Spangenberg, 1990) of needle-like silicon carbide fibers (whiskers) penetrate the cell wall to permit injection or uptake of DNA into cells (Kaeppeler et al., 1990).
4. *Agrobacterium*-mediated transformation takes advantage of a genus of bacteria that infects plant cells and transfers long segments of DNA, which become integrated into the host plant genome.

Scientists can splice genes of interest into the transferred DNA (Gohlke and Deeken, 2014). Regardless of the mechanism of delivery, once inside the cells, DNA may integrate into the genome and be expressed, thereby potentially introducing new traits into the recipient plant (Zupan and Zambryski, 1995).

Transgenesis can also be used to induce mutations or alter the function of native genes. Loss-of-function mutations may occur when a sequence is inserted into a gene, and the gene function is thereby inactivated. Alternatively, gain-of-function mutations are created when an active sequence element, such as a promoter or enhancer, is inserted near a functional gene, causing an increase in the transcription of the target gene, which can lead to a novel or enhanced phenotype. Large numbers of transformation events are needed to screen for specific kinds of mutations in specific genes. Fortunately, large numbers of trees can be outplanted and maintained as a field archive, so that mutations can be expressed for mature traits in addition to juvenile ones (Busov et al., 2005a).

(Continued)

BOX 3-3 Continued

Cisgenesis

Cisgenesis is similar to transgenesis, but the inserted genes or DNA fragments are from an organism that is sexually compatible with the recipient organism. That is, the incorporation of the DNA into the target cell could possibly be accomplished with selective breeding, but biotechnology tools allow for the direct introduction of the related DNA into the cell to achieve expression of the desired genetic trait.

RNA Interference

RNA interference is a molecular strategy common to all higher organisms for defense against parasites and pathogens, and regulation of native gene expression. Aspects of this natural process can be engineered to shut off (“silence”) specific genes in the parasite, insect, pathogen, or host plant by incorporating a small piece of the gene sequence in a configuration that results in the production of double-stranded RNA; this in turn activates the “dicer” complex, which degrades transcripts that match the gene fragment (Tang et al., 2003).

Genome Editing

Genome editing is a genetic modification process that makes specific and targeted changes to an organism’s DNA. The four main classes of this approach are meganucleases, zinc finger nucleases, transcription activator-like effector nucleases (TALENs), and the clustered regularly interspaced short palindromic repeat (CRISPR) nuclease system. The CRISPR system generates fewer “off-target” changes and thus has become the favored approach among researchers (Iyer et al., 2018). The CRISPR toolbox is rapidly expanding as researchers develop innovative methods to manipulate this system (Wang et al., 2016), which has opened the door to using genome editing to introduce robust disease resistance genes into plants (Langner et al., 2018).

Genome editing by CRISPR has significant potential for introducing specific changes in the genes of forest trees (Tsai and Xue, 2015; Elorriaga et al., 2018). For example, CRISPR editing in Chinese white poplar (*Populus tomentosa*) has been reported for a phytoene desaturase (*PDS*) gene, giving rise to albino phenotypes (Fan et al., 2015). CRISPR technology may make it possible to create homozygous biallelic DNA sequence changes (Gantz and Bier, 2015), which would eliminate the need to intercross modified trees to ensure that the edited gene was in a homozygous state. This is a significant advantage for trees, which typically have long generation times and poor tolerance for inbreeding.

Synthetic DNA

Synthetic DNA refers to genes produced in the laboratory that are not based on any naturally occurring DNA sequences but that may have functional properties or utility for genetic engineering. They are different from naturally occurring genes in that they may be made or found to have unique metabolic functions. Synthetic genes are different from genes that are artificially synthesized but are based on known genes from any living microbe, plant, or animal. At the time the committee wrote its report, no truly synthetic genes had been introduced into a forest tree. In the future, novel synthetic genes could be of value for forest health, particularly for generating highly specific resistance to attacks by insect pests and pathogens if and when natural resistance genes are overcome by newly evolved variants of pests or pathogens. The committee is aware of the possibility of the eventual creation of such novel synthetic genes; however, the relevance to this report is purely hypothetical.

^aIn the U.S. regulatory system, chemical mutagenesis is not a regulated process.

To use biotechnology to confer resistance to a forest health threat, the first step would be to identify the gene that would be targeted for modification, introduction, or silencing. If a gene target is not already in hand, then a gene discovery process would be required. This step has traditionally been hindered in trees due to the characteristics that make them difficult as experimental organisms: large size, long generation time, potentially weak correlations between seedling and adult phenotypes, and (in the case of conifers) immense genomes. Purification of high-quality genomic DNA from forest trees requires modest modifications of standard procedures used for extracting DNA from plants due to high phenolic content, large fragile

cells, or highly lignified tissue, such as stems or inner bark. The sheer size of many tree genomes presents a less tractable problem. Conifers have some of the largest genomes ever sequenced. The pine genomes can exceed 20,000 megabase pair (Mbp) per haploid genome (Zimin et al., 2014); sugar pine (*Pinus lambertiana*) has a genome size of 31,000 Mbp (Stevens et al., 2016). In comparison, *Arabidopsis* has only 135 Mbp and rice has 420 Mbp per haploid genome. Huge genome sizes and high content of repetitive DNA present difficulties in DNA sequencing and in genome assembly after sequencing.

Another problem results from the sequence diversity of forest tree genomes. Forest trees have high levels of heterozygosity due to their large population sizes and outcrossing breeding systems (Williams et al., 1999; Remington and O'Malley, 2000). There are no inbred lines of forest trees and few, if any, haploid individuals. Consequently, sequencing a tree genome is made more difficult because, even for an individual tree, there are two diverse haploid genomes that are being sequenced at the same time, creating a challenge for sequence assembly. In sequencing and assembling the loblolly pine (*Pinus taeda*) genome, direct sequencing of DNA from haploid megagametophyte seed storage tissue avoided this difficulty (Zimin et al., 2014). Unfortunately, the seed storage tissues of angiosperm (broad-leaved) forest trees (such as ash) are diploid or even polyploid, and so this strategy is not available.

Genome sequences can provide substantial insights into organismal evolution, but their applicability in biotechnological approaches requires functional characterization of the components of the genome, including transcribed sequences (genes) and regulatory elements. One of the most significant methods for learning about the function of tree genomes is comparative sequence analysis, which reveals homologous sequences in different genomes that, in turn, implies similar functions. Proof of function of homologs requires further testing, such as evidence of transcription and translation, purification of a functional product, or genetic complementation. Here again, forest trees are at a severe disadvantage. Many advances in functional genomics have come from work on the genetic model plant *Arabidopsis thaliana* and herbaceous crops such as maize. Many tree species have structural and developmental differences that either required adaptation of methodology or precluded application altogether. Furthermore, many characteristics common to trees (e.g., dormancy, wood formation, and obligate outcrossing) have few or no analogs in annual crop species.

Recent technological developments have mitigated some of these shortcomings such that dramatic progress has been made in understanding the organization, structure, and function of tree genomes, thereby facilitating potential biotech modifications aimed at pressing problems in forest health. These developments include large-scale quantitative trait locus (QTL) or genome-wide association studies coupled with in-depth analyses of transcriptional and metabolic responses to insect or pathogen attack. Additionally, genome editing can produce a “meiotic drive” (a kind of gene drive) function that converts a heterozygous individual to a homozygous one at one or more loci of interest, eliminating a generation of selfing to produce homozygous trees in one generation (see Box 3-4).

The second phase of deployment in using biotechnology to modify phenotypes is production of trees containing the desired gene sequence. Transgenesis and genome editing require a transformation and tissue culture protocol in which the desired modification can be introduced into a single cell (usually in callus culture), and whole plants are generated from the transformed cell by regeneration of roots and shoots from disorganized callus tissue (organogenesis) (Birch, 1997). Many species of trees remain recalcitrant to the process of cell culture and regeneration. Even when regeneration is possible, the regeneration of a plant from a single cell may not produce an individual that has the desired genetic change in every cell. In well-studied plant species that are amenable to this process, embryos can be produced through somatic embryogenesis, a process where the manipulated cell or cells originate from a totipotent embryo and then are induced to make more embryos (Hakman and Von Arnold, 1985; Suprasanna et al., 2005). Regeneration can be stepwise and sequential, where shoots are induced first and rooting is induced subsequently through organogenesis. This process is complex and must be customized not only at the species level but often for individual cultivars within a species (Busov et al., 2005a). The third phase is field testing. The case study species demonstrate varying degrees of progress with regard to the application of biotechnology to mitigating forest health threats (see Box 3-5).

BOX 3-4 Status of Gene-Drive Feasibility in Trees

A gene drive is a system of biased inheritance in which the ability of a genetic element to pass from a parent to its offspring through sexual reproduction is enhanced, resulting in a preferential increase of a specific genotype that determines a specific phenotype in a population (NASEM, 2016). It can occur in nature (e.g., in mosquitoes and mice), and as of 2018, scientists were studying this process and others to develop engineered gene drives in various organisms. Introducing gene drives into an organism's population may be of interest to reduce disease (e.g., to reduce the ability of mosquitoes to carry or transmit infectious diseases) or to control nonnative species. In trees, gene drives might be of interest to ensure the passage of resistance to a disease or insect from a modified tree on to the next generation.

However, as of 2018, research into gene drives was still nascent, and much remained to be learned about the processes and possible impacts before employing their use outside the laboratory. Trees are not good candidates for gene drive research because of their long generation times (NASEM, 2016). The insect pests that affect trees would be better subjects for research because of their short generation times; however, the potential effects on forest health from the modification of insects was outside the committee's statement of task.

BOX 3-5 Progress in Using Biotechnology to Confer Resistance to Case Study Species

American Chestnut

Building on work begun in the 1990s, the genes, transfer vectors, and technology for using biotechnology in the American chestnut has been developed (Merkle et al., 1991; Polin et al., 2006; Andrade et al., 2009; Barakat et al., 2009, 2012; Jabr, 2014; Newhouse et al., 2014a,b; Powell, 2014). The most promising candidate gene for genetic resistance to chestnut blight was a wheat gene encoding the enzyme oxalate oxidase (OxO) (Polin et al., 2006; Welch et al., 2007). Oxalic acid ($C_2H_2O_4$) is generated by the blight fungus during infection. The acid environment weakens plant cell walls, enabling other fungal enzymes to degrade the wall and the cell membranes, killing the cell (Dutton and Evans, 1996; Welch et al. 2007). In plants naturally possessing an OxO gene, oxalate oxidase catalyzes the degradation of oxalic acid by converting it to carbon dioxide and hydrogen peroxide. The protein encoded by the OxO gene from wheat is effective against oxalic acid in tissues of the American chestnut and shows no evidence of toxicity to the host plant.

Transgenesis using *Agrobacterium*-based vectors have successfully transferred OxO genes into the American chestnut (Andrade et al., 2009; Zhang et al., 2011). A fast and accurate in vitro leaf assay was developed to detect OxO activity in the leaves of transformed and regenerated plants early in plant development (Newhouse et al., 2014a). Investigators have now shown that transfer and expression of a wheat OxO gene in the American chestnut confers a degree of resistance equivalent to or greater than that found in the Chinese chestnut (Zhang et al., 2013; Newhouse et al. 2014a). The OxO-transformed plants derived from the original transformant are named "Darling" American chestnut trees after Herbert Darling, former president of the New York Chapter of TACF. The Darling 58 genotype has been characterized for blight resistance, growth and form, nutritional composition, lack of toxicity to the host plant, stability of blight tolerance, nontarget interactions, and lack of effects on target organisms (see Figure 3-6; Newhouse, 2018).

Whitebark Pine

No effort to date has focused on utilizing biotechnology to impart genetic resistance in whitebark pine. The large genome size of conifers, limited information on the genome of whitebark pine and candidate resistant genes, and biotechnology tools available suggest using biotechnology would take perhaps a decade or much longer to produce a resistant tree. With resistance breeding in whitebark pine imparting a more immediate and cost-effective solution, there may be little need to explore this option for whitebark pine, unless (a) the resistance(s) identified in the selective breeding method prove to be not durable (e.g., evolution of virulence in the pathogen), (b) some populations (seed zones) of whitebark pine have little or no inherent resistance and using seedlots from other seed zones is deemed not suitable for the environmental conditions to which they would be moved, or (c) additional unique types of resistance were identified (not found in current whitebark pine) and deemed necessary to complement the current resistance from breeding to help ensure that the trees stay resistant into the future. Even if biotechnology is used, the seed production would likely be through the development of seed orchards, which would add at least two decades to the production of resistant seed.

(Continued)

BOX 3-5 Continued



FIGURE 3-6 Wild-type American chestnut seedlings (left), Darling transgenic American chestnut seedlings (middle), and Chinese chestnut seedlings (right). SOURCE: Bill Powell, SUNY-ESF. Available at http://parrottlab.uga.edu/SIVB/HTML/Darling%2054%20American%20chestnut%20small%20stem%20assay%209-11-15%20SUNY-ESF%20DSC_0160.html.

A potential advantage of biotechnology for whitebark pine is that it may be possible to develop seedlots with a higher frequency of resistant seedlings than in the initial generation of parent trees now being used. However, it may be simpler and more efficient to plan to plant extra seedlings from the selective-breeding resistance program (perhaps only 20 to 40 percent of seedlings from any current resistant parent tree will be rust resistant). Perhaps the real potential (future) utility of biotechnology for developing resistant whitebark pine would be if new types of genetic resistance (of a durable nature), not found in whitebark pine were identified and transferred into whitebark pine. Although researchers are cautiously optimistic about the durability of genetic resistance to the rust that is developed through the selective breeding program, knowledge of a backup option, provided through biotechnology, would be useful to have. Significant research and trials of this material would likely take one to several decades for any future deployment.

Ash

Protocols for applying biotechnology to North American ash have not been established. Micropropagation techniques are reported for European common ash (*F. excelsior*), narrow leafed ash (*F. angustifolia*, native to southern Europe, northwest Africa, and southwest Asia), and green, white, and black ash (Hammatt, 1994; Schoenweiss and Meier-Dinkel, 2005; Capuana, 2012; Beasley and Pijut, 2013; Li et al., 2014; Lee and Pijut, 2017). Successful *Agrobacterium*-mediated transformation is reported for green, white, and pumpkin ash (*F. profunda*) (Du and Pijut, 2009; Stevens and Pijut, 2014; Palla and Pijut, 2015). The lack of reports on the successful insertion and stable expression of a gene or genes effective against the emerald ash borer (EAB) are due, in part, to a lack of vetted genes. As of 2018, there was not an active program in the United States to develop reproducible and stable transformation systems for *Fraxinus*, although a stable micropropagation protocol suitable for gene transfer applications had recently been developed for both *F. pennsylvanica* (Li et al., 2014) and *F. Americana* (Merkle et al., 2017).

Pijut and her colleagues mention studies under way for insertion of the Cry8Da protein of the bacterium *B. thuringiensis* into *F. pennsylvanica* and other *Fraxinus*, but there are no reports in the literature or in the patent databases of success, as defined by integration of the gene into the genome, expression of the gene, and efficacy of the gene product against EAB. Toxicity studies have shown some efficacy of Cry8Da formulations against EAB adults when the preparation is sprayed on leaves (Bauer and Londoño, 2010). Toxicity tests on larvae await the development of an artificial diet that results in normal growth. The only alternative is to transform a susceptible ash, prove that the gene is expressed, grow the transformant to a suitable size, bud

(Continued)

BOX 3-5 Continued

graft to save the genotype and enable replicated studies, tape EAB eggs on the saplings, and track the fate of each hatched egg when the stem is dissected 8 weeks after taping (Koch et al., 2015). This testing process requires 8–10 years, assuming that the transformation system requires 4–5 years to develop and deploy. This transformation system estimate is less than the time actually required for development of a reliable micro-propagation and successful transformation system for American chestnut (Merkle et al., 1991; Carraway and Merkle, 1997; Andrade et al., 2009; Kong et al., 2014).

There are no reports on efforts to use genome-editing techniques in *Fraxinus* due to insufficient knowledge of the gene expression networks involved in defensive responses. Recent studies have featured deep sequencing transcriptome analyses, proteomes, and metabolomes in phloem or leaf tissues in other tree species (Hamanishi et al., 2015; Fu et al., 2016; Wu et al., 2016; Nguyen et al., 2017), but there are few studies in angiosperm trees that capture the transcriptome, proteome, and metabolome associated with response to stem-boring insects. Comparison of the defensive enzymes and metabolites in the phloem tissues of Manchurian ash (*F. mandshurica*) and black ash reveal few qualitative differences in either constitutive or induced phenolics, despite the resistance of Manchurian ash and the susceptibility of black ash (Whitehill et al., 2012). Studies of EAB larvae fed on Manchurian, green, and white ash reveal similar levels of detoxification enzymes in the insect regardless of the species food source, even though the phloem phenolic profiles of Manchurian ash differ considerably from the green ash and white ash (Cipollini et al., 2011). The most informative study, focused on a more detailed investigation of uninfested Manchurian ash and black ash, showed higher levels of peroxidases, lignin polymerization, and quinone generation in Manchurian ash (Rigsby et al., 2016). Based on these studies, peroxidases, lipoxygenases, chitinases, polyphenol oxidases, and other defense-related enzymes are expected in the proteome profiles of uninfested Manchurian ash. The defensive enzyme and metabolite profiles of infested and uninfested Manchurian ash and black ash subjected to water stress indicated nonqualitative changes in metabolites in both species, including a higher accumulation of pinoresinol A in infested Manchurian ash only when both species were not subjected to water stress (Chakraborty et al., 2014). The transcriptomes, proteomes, and metabolomes of the North American *Fraxinus* remain uninvestigated in controlled experiments, wherein genotypes of the same species grafted and grown at the same time are compared, infested versus uninfested. Once phenotyping strategies and statistical designs have sufficient power to identify differences in defensive responses directly attributable to EAB attack, genome-editing approaches could be possible provided that micropropagation and transformation techniques for North American *Fraxinus* are improved at the same time.

Poplar

There have been several notable developments in the genomics of the *Sphaerulina-Populus* pathosystem. The genomes of both the main host (*P. deltoides*) and the fungus have been sequenced by the U.S. Department of Energy's Joint Genome Institute (Dhillon et al., 2015). The fungal genome sequencing project also included the closely related *Sphaerulina populicola*, which does not cause cankers and has a broader host range within *Populus*. Both genomes are approximately 30 Mbp and contain about 10,000 genes in highly collinear and syntenic order. Genes that are specific to *S. musiva* are enriched for wood-degrading enzymes. Furthermore, *S. musiva* contains a co-regulated gene cluster that was apparently horizontally transferred from *Penicillium* fungus. This cluster is induced upon exposure to *Populus* wood and encodes genes with phyto-toxic, antifungal, and antibacterial activities (Dhillon et al., 2015).

There have also been a number of functional genomics studies of *S. musiva* in recent years that have provided additional insights into the infection process. For example, an RNAseq study revealed a potential fungal elicitor (SMEcp2) that is expressed during the infection process. Treatment of stems of susceptible individuals with the isolated protein caused lesions, suggesting that this elicitor induces necrosis in the host (Dunnell, 2016). Bioinformatic analysis of the genome sequences revealed another secreted peptide (RALF27) that is present in both *S. populicola* and *S. musiva*, but absent in other closely related fungi. In fact, the closest match in public databases is to the RALF27 gene of *P. deltoides*, suggesting another case of horizontal transfer, but this time from host to fungus, potentially enhancing virulence (Thynne et al., 2017).

(Continued)

BOX 3-5 Continued

On the host side, an RNAseq analysis in hybrid *Populus* demonstrated up-regulation of genes involved in oxidation-reduction, protein fate, secondary metabolism, and defense-related gene products, all of which is consistent with expectations. However, genes related to the hypersensitive response were also up-regulated in susceptible host genotypes, supporting the hypothesis that susceptibility to this necrotrophic pathogen may be enhanced by triggering programmed cell death in the host (Liang et al., 2014). Similar results were observed in *P. deltoides*, for which the jasmonate and ethylene signaling pathways were induced in response to infection with *S. musiva*, along with genes involved in lignin biosynthesis and cell wall modification (Foster et al., 2015).

One of the reasons that *Populus* has become a favored model organism is the ease with which it is maintained and propagated in tissue culture and from vegetative cuttings. This facilitates the development and large-scale implementation of biotechnology-based methods of tree improvement (Busov et al., 2005a). Early efforts focused on developing spontaneous mutants in tissue culture with enhanced resistance to *S. musiva*, but these results translated poorly from the greenhouse to the field (Ostry and Ward, 2003). Targeted attempts to enhance host resistance with *Agrobacterium*-mediated transformation have been more successful. Overexpression of the antimicrobial peptides AMP1.2 and ESF12 enhanced resistance of a hybrid *Populus* clone to *S. musiva* based on a leaf disk assay (Liang et al., 2002). Similarly, overexpression of the Oxo gene from wheat in hybrid *Populus* increased resistance to leaf infection by *S. musiva* (Liang et al., 2001). This recapitulates the success with this gene against the chestnut blight, *Cryphonectria parasitica*. However, unlike the chestnut results, the *Populus* transgenics have not yet been tested in the field, and efficacy against cankers has not yet been demonstrated.

A method developed to transform *S. musiva* using *Agrobacterium* (Foster et al., 2014) holds great promise to enhance understanding of the infection process and possibly to provide control measures aimed at the fungus using gene drives (Gantz et al., 2015). For example, following the sequencing of the black cottonwood (*Populus trichocarpa*) genome (Tuskan et al., 2006), it became possible to tag genes by insertional mutagenesis to identify the sites of insertion and to isolate the genes that activated to produce a phenotype (Busov et al., 2005b). Three types of insertional mutagenesis have been carried out for poplars. Mutagenesis by insertion of T-DNA from *Agrobacterium* (Fladung et al., 2004; Busov et al., 2005b), insertion of a maize Ac transposable element (Howe et al., 1991), and insertion of reporter genes that are activated when inserted near a promoter or an expression enhancer (enhancer traps) (Groover et al., 2004). Enhancer traps are sequences containing a low-expression reporter gene that is activated if inserted near the promoter of an active gene, giving rise to a reporter gene phenotype (Springer, 2000).

TIME LINES AND COSTS OF DIFFERENT MANAGEMENT OPTIONS FOR FOREST HEALTH

The speed and cost of approaches to mitigate threats to forest health can vary widely. They are variable not only by approach (e.g., biological control, breeding, or biotechnology) but also by the state of knowledge about the target tree and the target pest (and its potential predator).

Speed and Cost of Biological Control

The speed and cost of biological control efforts vary depending on the biology of the target pest and the availability of biocontrol agents. A best-case scenario might be represented by the ash whitefly (*Siphoninus phillyreae* Haliday), an exotic insect from Eurasia and Africa that caused extensive defoliation of urban ornamental trees in California between 1988 and 1991 (Pickett et al., 1996). A wasp parasitoid, *Encarsia inaron* Walker, was imported from Italy and Israel, reared and tested under confined conditions, and then released into 43 counties in California by 1992. This resulted in nearly total control of the ash whitefly within the first year, with populations in Riverside, California, being reduced by a factor of 10,000 (Bellows et al. 1992). The total investment for this program was estimated at \$1.2 million, and the cost savings were estimated to be between \$220 million and \$300 million, based primarily on the retail cost of removing and replacing urban trees (Pickett et al., 1996). This case was simpler than average for several reasons. First, the insect was restricted to California, and so federal regulations about interstate movement

were not a factor, and only one state regulatory agency and USDA were involved. Second, the parasitoid was readily available and highly specific, so the risk assessment was simplified. A more typical biological control effort could be expected to cost between \$2 million and \$5 million and take 5–10 years to complete (Dr. Mark Hoddle, University of California, Riverside, personal communication, August 20, 2018). Other biocontrol efforts may not be successful, as has been the case for EAB (see Box 3-1). Additionally, the introduction of nonnative predators to control nonnative pests can often take years, first to identify the appropriate predators and second to obtain regulatory approval for their use (Rose, 2018).

Speed of Selective Resistance Breeding

The time line for selective resistance breeding in forest trees is dependent on several factors. In the best-case scenario for selective breeding, the infrastructure for a breeding program already exists, tree breeding expertise exists, and the biology of the tree species and the insect or pathogen is known. As discussed above (see section “Breeding to Enhance Resistance”), the first steps in selective breeding are to determine whether there is genetic resistance within the affected species, the frequency of resistance over its range, and type and degree of resistance available (i.e., is it immediately useable or will breeding be required?).

Determining the frequency and distribution of resistance, where it exists, may take several years or decades. Seed collection and testing of seedlings from hundreds or thousands of parent trees may be necessary. Those steps must then be followed with the development of breeding or orchard populations that have useful types and degrees of genetic resistance and sufficient genetic diversity to use for restoration (e.g., Sniezko et al., 2012; Dudley et al., 2017).

Two of the fastest evolving selective-breeding programs in forest trees have been development of resistance to the soilborne pathogen *Phytophthora lateralis* in Port-Orford-cedar (*Chamaecyparis lawsoniana*) on the West Coast (Sniezko et al., 2012) and development of resistance to the fungal disease *Fusarium oxysporum* in the Hawaiian koa tree (*Acacia koa*; Dudley et al., 2017). However, these two operational resistance programs only progressed rapidly once the basic data about resistance had been collected. In Port-Orford-cedar, the initial assessment erroneously concluded that there was no resistance (Hansen et al., 1989). In the koa, there was initial uncertainty as to the causative agent of mortality. The operational program for resistance in Port-Orford-cedar started in 1996 (after a significant research period), and the first orchard seed was released by 2003. The operational koa wilt resistance program started in 2003; the first orchard seed was not available until over a decade later. Even though programs for these two species were producing resistant seed as of 2018, the work was not complete. Seed was available for only some breeding zones, and the number of resistant parent trees in some orchards is too low to ensure that genetic diversity is preserved.

By contrast, the program to develop white pine blister rust resistance in sugar pine has taken longer to develop because of lower degrees of resistance and the longer time to reproductive maturity in sugar pine. The sugar pine resistance breeding program has continued for 50 years, with slow but steady progress (Sniezko et al., 2000; Kegley and Sniezko, 2004; McDonald et al., 2004; Kinloch et al., 2008, 2012).

The case of whitebark pine with resistance to white pine blister rust demonstrates the variation in the time it takes from resistant parent identification to deployment of resistant seedlings based on geography and parent genetics (Sniezko et al., 2007, 2011). Six restoration plantings were established in Crater Lake National Park from 2009 to 2016 (see Figure 3-7), using seedlings from some of the most resistant parents from the park. Seedling testing of progeny of Crater Lake parent trees was started in 2004, making the time from first testing to the first restoration planting only 5 years. However, seed orchards are also planned for Oregon and Washington seed zones, and in this case it may take from 10 to 20 years before resistant seed from these orchards is available. Thus, the overall time to begin restoration efforts using selective resistance breeding with whitebark pine can vary from as little as 5 years to several decades or more. The highly sporadic nature of good cone crops can also slow progress in resistance testing of candidate trees. Even in the case of Crater Lake, additional parent trees are being evaluated to increase the genetic base of seedlots used for restoration. With enough funding, a good cone crop, and a good seed collection effort, hundreds or even thousands of whitebark pine parent trees could be evaluated in a short time.



FIGURE 3-7 Restoration planting of whitebark pine (established 2009) at Crater Lake National Park. PHOTO CREDIT: R. Sniezko.

The backcross breeding program for the American chestnut which occurred over six generations took 35 years, a relatively short amount of time for several generations of tree breeding (see Figure 3-2). However, the program did not include the establishment of resistant seed orchards, the incorporation of genetic diversity in resistant seeds, or the development of resistant populations of chestnut for different geographic areas.

Relative Speed and Cost of Biotechnological Approaches in Trees

One of the commonly cited advantages of biotechnological approaches to create resistant genotypes of trees is the speed with which they can be deployed. Selective breeding and backcrossing are slow processes in some tree species (such as sugar pine) because the low initial degree of resistance and the long juvenile periods of most trees translate to long generation times and therefore very slow breeding cycles (Harfouche et al., 2012; Isik et al., 2015). Furthermore, there is often a poor correlation between traits measured in juvenile trees compared to those in mature trees, which necessitates expensive field testing over multiple years for each breeding cohort (White et al., 2007). Consequently, most forest breeding programs have only progressed through a few of generations, leading to modest genetic gains compared to annual commodity crops such as maize and wheat (Isik et al., 2015). Biotechnology has been promoted as a means to accelerate the domestication of forest trees by shortening the breeding cycle (e.g., through early flowering; Martín-Trillo and Martínez-Zapater, 2002; Flachowsky et al., 2009), using marker-aided selection (Harfouche et al., 2012; Isik et al., 2015), or bypassing breeding entirely by manipulating DNA (Merkle and Dean, 2000; Harfouche et al., 2011).

The actual speed of biotechnological approaches depends on a number of practical factors that can potentially limit implementation. In the area of marker-aided selection, it is becoming increasingly clear that the efficacy of this approach is limited by the complex genetic architecture of quantitative traits. Genome-wide association studies have clearly demonstrated that complex traits are polygenic, that is, controlled by hundreds or even thousands of loci, each of which has small genetic effects, and complex epistatic interactions (Boyle et al., 2017). This complexity means that alleles that control traits in one population are often not effective at predicting phenotypes in an unrelated population, thus requiring expensive and time-consuming marker discovery and model training in each subpopulation (Resende et al., 2012). Although this problem should be diminished for some disease resistance traits with simpler genomic architecture (e.g., for cases of major gene resistance), these types of resistance are expected to be less durable than quantitative resistance based on multiple unlinked loci (McDonald and Linde, 2002), so applications are limited.

The situation could be different when using biotechnology to make individual genetic modifications to produce dramatic phenotypic changes. For example, introduction of the crystalline endotoxins derived from *Bacillus thuringiensis* (*Bt*) can confer complete resistance to feeding by Lepidoptera (moths and butterflies), even in host species that are normally highly susceptible to such damage (Shelton et al., 2002). A wide variety of *Bt* toxins are already available (de Maagd et al., 2003), and existing toxins can be modified using mutagenesis to enhance efficacy against a particular insect once introduced into the plant via transgenesis (de Maagd et al., 1999). Similar examples exist for pathogen resistance as well, such as the introduction of the oxalate oxidase gene (see Box 3-5), which shows broad efficacy against fungal pathogens such as the *Cryphonectria* blight in American chestnut (Zhang et al., 2013) and *Septoria* leaf spots in *Populus* (Liang et al., 2001). Nevertheless, the relative speed with which biotechnology solutions can be implemented depends on a number of factors, and significant impediments at each stage of development could substantially slow the process.

As reviewed above (see section “Using Biotechnology to Enhance Resistance”), the first step to make use of biotechnology to introduce genetic resistance is gene identification. Although the gene discovery process has become remarkably more efficient with advances in genome sequencing technology, this step could take a number of years. For example, in the case of the emerald ash borer, there was no genome or transcriptome sequence available for the insect or host in the early stages of the epidemic, and it is time-consuming and difficult to measure ash tree resistance, which requires infestation of trees that are 2–3 years old (Koch et al., 2015).

The second step is producing trees with the desired gene sequence. Under the best-case scenario, represented by the model transformation clones in *Populus*, it takes 4–8 months to produce transformed plants that could be transplanted to pots (Busov et al., 2010). At least another several months would then be required to vegetatively propagate enough material for a field trial. In other species for which transformation systems are not readily available, the process of regenerating a plant from somatic embryos to a seedling growing under ordinary conditions in a greenhouse can take more than 1 year. If the introduced gene is present in the germ line, progeny of the transformed plant will also have the inserted gene. In many tree species it can take 5–10 years or more until flowers are produced and the gene can be passed on to the next generation.

The third step is field testing. The length of this phase would depend on the growth rates of the trees and the life history of the insect pest or pathogen. In some cases, resistance is best evaluated in adult trees, which requires many years. For example, both *Septoria* and *Cryphonectria* cankers take years to develop, though effective in vitro assays have been developed for both diseases (LeBoldus et al., 2010; Newhouse et al., 2014b). Furthermore, multiple field trials over a large geographic area are desirable, especially in cases where significant genotype \times environment interactions occur for host susceptibility. Given the expense and difficulty of performing field trials, testing would typically begin on a limited basis to demonstrate efficacy before scaling up to larger and more widespread trials. This slow rollout would add years to the process. As a result, the full process would take over a decade.

Estimating costs of the application of biotechnology for forest health is difficult because it requires estimation of processes and products that have not yet been developed or information that is proprietary and not available. The cost of gene identification or developing a new DNA transfer system is undefined because in some cases the efforts could be unsuccessful; therefore, the project could have high costs with no results. Producing trees with the desired gene sequence through clonal propagation can be expensive.

However, when it comes to a comparison of costs between breeding and biotechnology, the costs may be similar or at least similarly variable. With regard to the identification of a trait of interest, for the biotech tree the expense is in gene discovery and integrating the desired change into the tree’s DNA; for breeding, the costs are related to screening and testing to find resistance. For both approaches, the costs can vary widely depending on the biology of the tree and the pest, the state of knowledge about the tree and pest biology, and the robustness of the biotech or breeding program associated with the species of interest. When it comes to the next step of clonal propagation, the costs are likely to be similar between the two approaches.

The major difference in costs between the two would be those associated with any regulatory approval that a biotech tree may need to obtain; a selectively bred or hybrid tree does not have to go through a regulatory process in the United States.

CONCLUSIONS AND RECOMMENDATIONS

Management to mitigate damage to forests from insects or pathogens takes significant time and resources. With regard to nonnative insects and pathogens, the first line of defense is preventing their introduction. When introduced pests have become established or native pests are expanding their range or increasing in virulence, there are a number of management options that may be employed, including taking no action. Chemical or biological control can control pests in some cases, but these approaches are often not acceptable to the public, effective, or timely. The development and actual deployment of genetic resistance, whether via breeding or biotechnology, will usually take decades from the initial research phase to even the beginning of the restoration plantings. However, given the repeated introduction of nonnative pests and the likelihood of continued abiotic stress from climate change, incorporating genetic resistance may be the effective strategy for the long term.

Conclusion: Substantial literature supports the need for sustained investment in prevention and eradication as the most cost-effective and lowest impact approaches for managing introduction of nonnative insect pests and pathogens.

Economic analysis has found that the United States could save billions of dollars in avoided impacts from nonnative pests by increasing its efforts to prevent the entry of nonnative pests. Inspection, quarantine, and treatment of imported materials can facilitate the interception of insect pests and pathogens prior to their potential escape and establishment.

Recommendation: Investment in effective prevention and eradication approaches should be the first line of defense against nonnative species in efforts to maintain forest health.

Conclusion: Any single management practice alone is not likely to be effective at combatting major pest outbreaks.

Site management practices—such as pesticide use, thinning, reintroduction of fire, and removal of infested trees—can minimize conditions that favor a pest outbreak. Biological control agents can suppress insect pest populations or mitigate the effects of a fungal pathogen. However, experience with the American chestnut, whitebark pine, ash, and poplar indicates that these practices will be insufficient to curtail the loss of affected tree species.

Recommendation: Management for forest health should make use of multiple practices in combination to combat threats to forest health.

Conclusion: A variety of biotech and nonbiotech approaches have been and will be developed to address insect pest and pathogen threats. The time line for use of these tools in management activities for forest trees and forest health will depend on a number of factors, but the biology of the species involved (both tree and insect or pathogen) and the environments in which the tree species exist will have a major influence on effective mitigation.

The time line for using approaches to mitigate forest health such as biological control, breeding, or biotechnology vary by the state of knowledge about the target tree and the target pest. The availability of natural enemies, the size of the tree genome, and the environment will also affect the deployment of mitigation tools.

Conclusion: Many tree species have some degree of resistance to particular native and nonnative pests that may be harnessed to combat infestations and epidemics.

It is often possible to find resistance to damaging insects and diseases in the field and use it to develop resistant trees for restoration planting. However, this outcome depends on the resources to find resistant trees and established breeding programs to develop resistant seedlings. This strategy has been successfully deployed for blister rust resistance in whitebark pine and, at the time of the committee's report, were also in use for ash against EAB. For whitebark pine, there are still no programs for drought tolerance or resistance to mountain pine beetle.

Recommendation: Entities concerned about forest health should devote resources to identifying resistant trees within a population that have survived a pest outbreak. Research to understand the role of resistance in coevolved systems from the perspective of a global host–pest system, where the nonnative pathogen or insect originate, would help guide efforts in North America.

Conclusion: Using biotechnology to introduce resistance to threats in forest trees has been hampered by the complexity of tree genomes, the genetic diversity in tree populations, and the lack of knowledge about genetic mechanisms that underlie important traits. However, recent technological developments have improved functional genomic tools, facilitating the potential for biotechnology to help address forest health problems.

At the time the committee was writing its report, there was insufficient knowledge about the fundamental mechanisms involved in resistance to pests to efficiently identify genomic means to mitigate pest damage. Most tree genomes had not been sequenced, and there were still many unknowns about the underlying nature of resistance, including its heritability and on whether it will be durable. Investigations in trees species are needed to uncover all forms of resistance, not just those due to easily discernible single major genes. Likewise, in using biotechnology, greater efforts are needed to understand what types of resistance or combinations of resistance are likely to be durable.

Recommendation: More research should be conducted on the fundamental mechanisms involved in trees' resistance to pests and adaptation to diverse environments, including a changing climate.

Conclusion: The time it takes to identify resistance in an affected population, breed resistant seedlings, and plant resistant seedlings in the field can vary from a few years to multiple decades, depending on the species. Incorporating resistance via biotechnology into a tree species is also a lengthy process, the duration of which varies by species.

The amount of natural genetic resistance in a population can vary by species or by the geographic distribution of a species, and the reproductive cycle of the tree will affect how quickly resistant offspring can be generated. When introducing resistance via biotechnology, the number of the genes involved in the expression of resistance will affect how long it takes to identify and incorporate resistance in biotech trees.

Recommendation: Sufficient investment of time and resources should be made to successfully identify or introduce resistance into tree species threatened by insects and pathogens.

REFERENCES

Abell, K.J., J.J. Duan, L. Bauer, J.P. Lelito, and R.G. Van Driesche. 2012. The effect of bark thickness on host partitioning between *Tetrastichus planipennisi* (Hymen: Eulophidae) and *Atanycolus* spp. (Hymen: Braconidae), two parasitoids of emerald ash borer (Coleop: Buprestidae). *Biological Control* 63(3):320–325.

- Ally, D., K. Ritland, and S.P. Otto. 2010. Aging in a long-lived clonal tree. *PLoS Biology* 8:e1000454.
- Anagnostakis, S.L. 2012. Chestnut breeding in the United States for disease and insect resistance. *Plant Disease* 96(10):1392–1403.
- Anagnostakis, S.L. and B. Hillman. 1992. Evolution of the chestnut tree and its blight. *Arnoldia* 52(2):3–10.
- Andrade, G.M., C.J. Nairn, H.T. Le, and S.A. Merkle. 2009. Sexually mature transgenic American chestnut trees via embryogenic suspension-based transformation. *Plant Cell Reports* 28(9):1385–1397.
- Arno, S.F., and R.J. Hoff. 1989. *Silvics of whitebark pine (Pinus albicaulis)*. Ogden, UT: U.S. Forest Service.
- Aubin, I., F. Cardou, K. Ryall, D. Kreutzweiser, and T. Scarr. 2015. Ash regeneration capacity after emerald ash borer (EAB) outbreaks: Some early results. *The Forestry Chronicle* 91(3):291–298.
- Barakat, A., D.S. Diloreto, Y. Zhang, C. Smith, K. Baier, W.A. Powell, N. Wheeler, R. Sederoff, and J.E. Carlson. 2009. Comparison of the transcriptomes of American chestnut (*Castanea dentata*) and Chinese chestnut (*Castanea mollissima*) in response to chestnut blight infection. *BMC Plant Biology* 9:51.
- Barakat, A., M. Staton, C.-H. Cheng, J. Park, N.B.M. Yassin, S. Ficklin, C.-C. Yeh, F. Hebard, K. Baier, W. Powell, S.C. Schuster, N. Wheeler, A. Abbott, J.E. Carlson, and R. Sederoff. 2012. Chestnut resistance to the blight disease: Insights from transcriptome analysis. *BMC Plant Biology* 12:38.
- Bauer, L.S., J.J. Duan, J.R. Gould, and R.G. Van Driesche. 2015. Progress in the classical biological control of *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) in North America. *The Canadian Entomologist* 147(3):300–317.
- Bauer, L.S., and D.K. Londoño. 2010. Effects of *Bacillus thuringiensis* SDS-502 on adult emerald ash borer. Pp. 74–75 in *Proceedings: 21st U.S. Department of Agriculture Interagency Research Forum on Invasive Species 2010*. Newtown Square, PA: U.S. Forest Service.
- Beasley, R.R., and P.M. Pijut. 2013. Regeneration of plants from *Fraxinus nigra* Marsh. Hypocotyls. *HortScience* 48(7):887–890.
- Belokobylskij, S.A., G.I. Yurchenko, J.S. Strazanac, A. Zaldívar-Riverón, and V. Mastro. 2012. A new emerald ash borer (Coleoptera: Buprestidae) parasitoid species of *Spathius* nees (Hymenoptera: Braconidae: Doryctinae) from the Russian Far East and South Korea. *Annals of the Entomological Society of America* 105(2):165–178.
- Bellows, T.S., T.D. Paine, J.R. Gould, L.G. Bezark, J.C. Ball, W. Bentley, R.L. Coviello, J. Downer, P. Elam, D. Flaherty, P. Gouveia, C. Koehler, R.H. Molinar, N.V. O’Connell, E. Perry, and G. Vogel. 1992. Biological control of ash whitefly: A success in progress. *California Agriculture* 46(1):24–28.
- Bentz, B.J., C.K. Boone, and K.F. Raffa. 2015. Tree response and mountain pine beetle attack preference, reproduction and emergence timing in mixed whitebark and lodgepole pine stands. *Agricultural and Forest Entomology* 17(4):421–432.
- Birch, R.G. 1997. PLANT transformation: Problems and strategies for practical application. *Annual Review of Plant Physiology and Plant Molecular Biology* 48(1):297–326.
- Boland, G.J. 2004. Fungal viruses, hypovirulence, and biological control of *Sclerotinia* species. *Canadian Journal of Plant Pathology* 26(1):6–18.
- Boyle, E.A., Y.I. Li, and J.K. Pritchard. 2017. An expanded view of complex traits: From polygenic to omnigenic. *Cell* 169(7):1177–1186.
- Burgiel, S., G. Foote, M. Orellana, and A. Perrault. 2006. *Invasive alien species and trade: Integrating prevention measures and international trade rules*. Washington, DC: Center for International Environmental Law and Defenders of Wildlife. Available at https://cleantrade.typepad.com/clean_trade/files/iastraderpt0106.pdf. Accessed November 8, 2018.
- Burnham, C.R. 1988. The restoration of the American chestnut. *American Scientist* 76(5):478–487.
- Busov, V.B., A.M. Brunner, R. Meilan, S. Filichkin, L. Ganio, S. Gandhi, and S.H. Strauss. 2005a. Genetic transformation: A powerful tool for dissection of adaptive traits in trees. *New Phytologist* 167(1):9–18.
- Busov, V., M. Fladung, A. Groover, and S. Strauss. 2005b. Insertional mutagenesis in *Populus*: Relevance and feasibility. *Tree Genetics & Genomes* 1(4):135–142.
- Busov, V., S.H. Strauss, and G. Pilate. 2010. Transformation as a tool for genetic analysis of *Populus*. Pp. 113–133 in *Genetics and Genomics of Populus*, S. Jansson, R. Bhalerao, and A. Groover, eds. New York: Springer.
- Capuana, M. 2012. In vitro propagation of ash (*Fraxinus excelsior* L.) by somatic embryogenesis. Pp. 213–221 in *Protocols for Micropropagation of Selected Economically-Important Horticultural Plants*, M. Lambardi, E.A. Ozudogru, and S.M. Jain, eds. New York: Springer.
- Carraway, D.T., and S.A. Merkle. 1997. Plantlet regeneration from somatic embryos of American chestnut. *Canadian Journal of Forest Research* 27(11):1805–1812.
- Carson, S.D., and M.J. Carson. 1989. Breeding for resistance in forest trees—a quantitative genetic approach. *Annual Review of Phytopathology* 27(1):373–395.

- Chang, S., E.L. Mahon, H.A. MacKay, W.H. Rottmann, S.H. Strauss, P.M. Pijut, W.A. Powell, V. Coffey, H. Lu, S.D. Mansfield, and T.J. Jones. 2018. Genetic engineering of trees: Progress and new horizons. *In Vitro Cellular & Developmental Biology-Plant* 54(4):341–376.
- Chakraborty, S., J.G.A. Whitehill, A.L. Hill, S.O. Opiyo, D.O.N. Cipollini, D.A. Herms, and P. Bonello. 2014. Effects of water availability on emerald ash borer larval performance and phloem phenolics of Manchurian and black ash. *Plant, Cell & Environment* 37(4):1009–1021.
- Choi, G.H., A.L. Dawe, A. Churbanov, M.L. Smith, M.G. Milgroom, and D.L. Nuss. 2012. Molecular characterization of vegetative incompatibility genes that restrict hypovirus transmission in the chestnut blight fungus *Cryphonectria parasitica*. *Genetics* 190(1):113–127.
- Cipollini, D., Q. Wang, J.G.A. Whitehill, J.R. Powell, P. Bonello, and D.A. Herms. 2011. Distinguishing defensive characteristics in the phloem of ash species resistant and susceptible to emerald ash borer. *Journal of Chemical Ecology* 37(5):450–459.
- Clapper, R.B. 1963. A promising new forest-type chestnut tree. *Journal of Forest* 61(12):921–922.
- Cohen, S.N., A.C.Y. Chang, H. Boyer, and R.B. Helling. 1973. Construction of biologically functional bacterial plasmids in vitro. *Proceedings of the National Academy of Sciences of the United States of America* 70(11):3240–3244.
- Cortesi, P. and M.G. Milgroom. 1998. Genetics of vegetative incompatibility in *Cryphonectria parasitica*. *Applied Environmental Microbiology* 64(8):2988–2994.
- Cudmore, T.J., N.B. Björklund, A.L. Carroll, and B.S. Lindgren. 2010. Climate change and range expansion of an aggressive bark beetle: Evidence of higher beetle reproduction in naïve host tree populations. *Journal of Applied Ecology* 47(5):1036–1043.
- de Maagd, R.A., D. Bosch, and W. Stiekema. 1999. *Bacillus thuringiensis* toxin-mediated insect resistance in plants. *Trends in Plant Science* 4(1):9–13.
- de Maagd, R.A., A. Bravo, C. Berry, N. Crickmore, and H.E. Schnepf. 2003. Structure, diversity, and evolution of protein toxins from spore-forming entomopathogenic bacteria. *Annual Review of Genetics* 37(1):409–433.
- Diller, J.D., R.B. Clapper, and R.A. Jaynes. 1964. Cooperative test plots produce some promising Chinese and hybrid chestnut trees. U.S. Forest Service Research Note NE-25. Upper Darby, PA: U.S. Forest Service.
- Dhillon, B., N. Feau, A.L. Aerts, S. Beauseigle, L. Bernier, A. Copeland, A. Foster, N. Gill, B. Henrissat, P. Herath, K.M. LaButti, A. Levasseu, E.A. Lindquist, E. Majoor, R.A. Ohm, J.L. Pangilinan, A. Pribowo, J.N. Saddler, M.L. Sakalidis, R.P. de Vries, I.V. Grigoriev, S.B. Goodwin, P. Tanguay, and R.C. Hamelin. 2015. Horizontal gene transfer and gene dosage drives adaptation to wood colonization in a tree pathogen. *Proceedings of the National Academy of Sciences of the United States of America* 112(11): 3451–3456.
- Du, N., and P.M. Pijut. 2009. *Agrobacterium*-mediated transformation of *Fraxinus pennsylvanica* hypocotyls and plant regeneration. *Plant Cell Reports* 28(6):915–923.
- Duan, J.J., L.S. Bauer, and R.G. Van Driesche. 2017. Emerald ash borer biocontrol in ash saplings: The potential for early stage recovery of North American ash trees. *Forest Ecology and Management* 394:64–72.
- Duan, J.J., G. Yurchenko, and R. Fuester. 2012. Occurrence of emerald ash borer Coleoptera: Buprestidae and biotic factors affecting its immature stages in the Russian Far East. *Environmental Entomology* 41(2):245–254.
- Duan, J.J., T.J. Watt, and K. Larson. 2014. Biology, life history, and laboratory rearing of *Spathius galinae* (Hymenoptera: Braconidae), a larval parasitoid of the invasive emerald ash borer (Coleoptera: Buprestidae). *Journal of Economic Entomology* 107(3):939–946.
- Dudley, N., T. Jones, R. James, R. Snieszko, J. Wright, C. Liang, P.F. Gugger, and P. Cannon. 2017. Applied genetic conservation of Hawaiian Acacia koa: An eco-regional approach. Pp. 78–91 in *Gene Conservation of Tree Species—Banking on the Future*, Proceedings of a Workshop, R.A. Snieszko, G. Man, V. Hipkins, K. Woeste, D. Gwaze, J.T. Kliejunas, and B.A. McTeague, tech. cords. Portland, OR: U.S. Forest Service.
- Dunnell, K.L. 2016. Understanding Host-Pathogen Interactions in the Sphaerulina musiva-Populus Pathosystem. Ph.D. dissertation, Oregon State University.
- Dutton, M.V., and C.S. Evans. 1996. Oxalate production by fungi: Its role in pathogenicity and ecology in the soil environment. *Canadian Journal of Microbiology* 42(9):881–895.
- Elorriaga, E., A.L. Klocko, C. Ma, and S.H. Strauss. 2018. Variation in mutation spectra among CRISPR/Cas9 mutagenized poplars. *Frontiers in Plant Science* 9:594.
- Fan, D., T. Liu, C. Li, B. Jiao, S. Li, Y. Hou, and K. Luo. 2015. Efficient CRISPR/Cas9-mediated targeted mutagenesis in Populus in the first generation. *Scientific Reports* 5:12217.
- Fettig, C.J., D.M. Grosman, and A.S. Munson. 2013. Advances in insecticide tools and tactics for protecting conifers from bark beetle attack in the western United States. Pp. 472–492 in *Insecticides—Development of Safer and More Effective Technologies*, S. Trdan, ed. Rijeka, Croatia: InTech.

- Fillatti, J.J., J. Sellmer, B. McCown, B. Haissig, and L. Comai. 1987. *Agrobacterium* mediated transformation and regeneration of *Populus*. Molecular and General Genetics 206(2):192–199.
- Finnoff, D., J.F. Shogren, B. Leung, and D. Lodge. 2007. Take a risk: Preferring prevention over control of biological invaders. Ecological Economics 62(2):216–222.
- Flachowsky, H., M.V. Hanke, A. Peil, S.H. Strauss, and M. Fladung. 2009. A review on transgenic approaches to accelerate breeding of woody plants: Review. Plant Breeding 128(3):217–226.
- Fladung, M., F. Deutsch, H. Hönicka, and S. Kumar. 2004. T-DNA and transposon tagging in aspen. Plant Biology 6(1):5–11.
- Foster, A.J., M.J. Morency, A. Séguin, and P. Tanguay. 2014. *Agrobacterium tumefaciens*–mediated transformation for targeted disruption and over expression of genes in the poplar pathogen *Sphaerulina musiva*. Forest Pathology 44(3):233–241.
- Foster, A.J., G. Pelletier, P. Tanguay, and A. Séguin. 2015. Transcriptome analysis of poplar during leaf spot infection with *Sphaerulina* spp. PLoS ONE 10(9):e0138162.
- Franceschi, V.R., P. Krokene, E. Christensen, and T. Krekling. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytologist 167(2):353–376.
- Fromm, M., L.P. Taylor, and V. Walbot. 1985. Expression of genes transferred into monocot and dicot plant cells by electroporation. Proceedings of the National Academy of Sciences of the United States of America 82(17):5824–5828.
- Fu, S., J. Shao, C. Zhou, and J.S. Hartung. 2016. Transcriptome analysis of sweet orange trees infected with “*Candidatus Liberibacter asiaticus*” and two strains of citrus tristeza virus. BMC Genomics 17(1):349.
- Gantz, V.M., and E. Bier. 2015. The mutagenic chain reaction: A method for converting heterozygous to homozygous mutations. Science 348:442–444.
- Gantz, V.M., N. Jasinskiene, O. Tatarenkova, A. Fazekas, V.M. Macias, E. Bier, and A.A. James. 2015. Highly efficient Cas9-mediated gene drive for population modification of the malaria vector mosquito *Anopheles stephensi*. Proceedings of the National Academy of Sciences of the United States of America 112(49):E6736–E6743.
- GAO (U.S. Government Accountability Office). 2015. Aquatic Invasive Species: Additional Steps Could Help Measure Federal Progress in Achieving Strategic Goals. Available at: <https://www.gao.gov/assets/680/673897.pdf>. Accessed June 18, 2018.
- Gohlke, J., and R. Deeken. 2014. Plant responses to *Agrobacterium tumefaciens* and crown gall development. Frontiers in Plant Science 5:155.
- Gonzales-Vigil, E., C.A. Hefer, M.E. von Loessl, J. La Mantia, and S.D. Mansfield. 2017. Exploiting natural variation to uncover an alkene biosynthetic enzyme in poplar. The Plant Cell 29(8):2000–2015.
- Gottschalk, K.W. 1993. Silvicultural Guidelines for Forest Stands Threatened by the Gypsy Moth. Radnor, PA: U.S. Forest Service.
- Gould, F., Z.S. Brown, and J. Kuzma. 2018. Wicked evolution: Can we address the sociobiological dilemma of pesticide resistance? Science 360(6390):728–732.
- Graves, A.H. 1942. Breeding work toward the development of a timber type of blight resistant chestnut. American Journal of Botany 29(8):622–626.
- Grente, J., and S. Sauret. 1969. L’hypovirulence exclusive, phénomène original en pathologie végétale. Comptes Rendus Hebdomadaire des Séances de l’Académie d’Agriculture de France. Série D 286:2347–2350.
- Grente, J., and S. Berthelay-Sauret. 1978. Biological control of chestnut blight in France. Pp. 30–34 in Proceedings of the American Chestnut Symposium, W.L. McDonald., F.C. Cech, J. Luchok, and C. Smith, eds. Morgantown: West Virginia University Press.
- Griffin, G.J. 2000. Blight control and restoration of the American chestnut. Journal of Forestry 98(2):22–27.
- Griffin, G.J., J.R. Elkins, D. McCurdy, and S.L. Griffin. 2006. Integrated use of resistance, hypovirulence, and forest management to control blight on American chestnut. Pp. 97–108 in Proceedings of Restoration of American Chestnut to Forest Lands, K.C. Steiner and J.E. Carlson, eds. Washington, DC: National Park Service.
- Groover, A., J.R. Fontana, G. Dupper, C. Ma, R. Martienssen, S. Strauss, and R. Meilan. 2004. Gene and enhancer trap tagging of vascular-expressed genes in poplar trees. Plant physiology 134(4):1742–1751.
- Gyenis, L., N.A. Anderson, and M.E. Ostry. 2003. Biological control of Septoria leaf spot disease of hybrid poplar in the field. Plant Disease 87(7):809–13.
- Haack, R.A., K.O. Britton, E.G. Brockerhoff, J.F. Cavey, L.J. Garrett, M. Kimberley, F. Lowenstein, A. Nuding, L.J. Olson, J. Turner, and K.N. Vasilaky. 2014. Effectiveness of the International Phytosanitary Standard ISPM no. 15 on reducing wood borer infestation rates in wood packaging material entering the United States. PLoS ONE 9:e96611.

- Haack, R.A., F. Hérard, J. Sun, and J.J. Turgeon. 2010. Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: A worldwide perspective. *Annual Review of Entomology* 55:521–546.
- Haas, S.E., M.B. Hooten, D.M. Rizzo, and R.K. Meentemeyer. 2011. Forest species diversity reduces disease risk in a generalist plant pathogen invasion. *Ecology Letters* 14(11):1108–1116.
- Hakman, I., and S. Von Arnold. 1985. Plantlet regeneration through somatic embryogenesis in *Picea abies* (Norway spruce). *Journal of Plant Physiology* 121(2):149–158.
- Hamanishi, E.T., G.L.H. Barchet, R. Dauwe, S.D. Mansfield, and M.M. Campbell. 2015. Poplar trees reconfigure the transcriptome and metabolome in response to drought in a genotype- and time-of-day-dependent manner. *BMC Genomics* 16(1):329.
- Hammatt, N. 1994. Shoot initiation in the leaflet axils of compound leaves from micropropagated shoots of juvenile and mature common ash (*Fraxinus excelsior* L.). *Journal of Experimental Botany* 45(6):871–875.
- Hansen, E.M., P.B. Hamm, and L.F. Roth. 1989. Testing Port-Orford-cedar for resistance to *Phytophthora*. *Plant Disease* 73(10):791–794.
- Harfouche, A., R. Meilan, and A. Altman. 2011. Tree genetic engineering and applications to sustainable forestry and biomass production. *Trends in Biotechnology* 29(1):9–17.
- Harfouche, A., R. Meilan, M. Kirst, M. Morgante, W. Boerjan, M. Sabatti, and G.S. Mugnozza. 2012. Accelerating the domestication of forest trees in a changing world. *Trends in Plant Science* 17(2):64–72.
- Hastings, F.L., E.H. Holsten, P.J. Shea, and R.A. Werner. 2001. Carbaryl: A review of its use against bark beetles in coniferous forests of North America. *Environmental Entomology* 30(5):803–810.
- Hebard, F.V. 2006. The backcross breeding program of the American Chestnut Foundation. *Journal of The American Chestnut Foundation* 19(2):55–77.
- Howe, G.T., S.H. Strauss, and B. Goldfarb. 1991. Insertion of the maize transposable element Ac into poplar. Pp. 283–294 in *Woody Plant Biotechnology*, M.R. Ahuja, ed. New York: Plenum.
- Huang, H., W.A. Carey, F. Dane, and J.D. Norton. 1996. Evaluation of Chinese chestnut cultivars for resistance to *Cryphonectria parasitica*. *Plant Disease* 80:45–47.
- Huber, D.P.W., S. Ralph, and J. Bohlmann. 2004. Genomic hardwiring and phenotypic plasticity of terpenoid-based defenses in conifers. *Journal of Chemical Ecology* 30(12):2399–2418.
- Isik, F., S. Kumar, P.J. Martinez-Garcia, H. Iwata, and T. Yamamoto. 2015. Acceleration of forest and fruit tree domestication by genomic selection. *Advances in Botanical Research* 74:93–124.
- Iyer, V., K. Boroviak, M. Thomas, B. Doe, L. Riva, E. Ryder, and D.J. Adams. 2018. No unexpected CRISPR-Cas9 off-target activity revealed by trio sequencing of gene-edited mice. *PLOS Genetics* 14(7):e1007503.
- Jabr, F. March 1, 2014. A new generation of American chestnut trees may redefine America's forests. *Scientific American* 310.
- Jacobs, D.F., H.J. Dalgleish, and C.D. Nelson. 2012. A conceptual framework for restoration of threatened plants: The effective model of American chestnut (*Castanea dentata*) reintroduction. *New Phytologist* 197(2):378–393.
- Jactel, H., and E.G. Brockerhoff. 2007. Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10(9):835–848.
- Jeffers, S.N., I.M. Meadows, J.B. James, and P.H. Sisco. 2012. Resistance to *Phytophthora cinnamomi* among seedlings from backcross families of hybrid American chestnut. Pp. 194–195 in *Proceedings of the Fourth International Workshop on the Genetics of Host-Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees*, R.A. Snieszko, A.D. Yanchuk, J.T. Kliejunas, K.M. Palmieri, J.M. Alexander, and S.J. Frankel, tech. cords. Albany, CA: U.S. Forest Service.
- Kaeppeler, H.F., W. Gu, D.A. Somers, H.W. Rines, and A.F. Cockburn. 1990. Silicon carbide fiber-mediated DNA delivery into plant cells. *Plant Cell Reports* 9(8):415–418.
- Kalaris, T., D. Fieselmann, R. Magarey, M. Colunga-Garcia, A. Roda, D. Hardie, N. Cogger, N. Hammond, P.T. Martin, and P. Whittle. 2014. The role of surveillance methods and technologies in plant biosecurity. Pp. 309–337 in *The Handbook of Plant Biosecurity*. Dordrecht, The Netherlands: Springer.
- Keane, R.E., and R.A. Parsons. 2010. Management guide to ecosystem restoration treatments: Whitebark pine forests of the northern Rocky Mountains, U.S.A. Fort Collins, CO: U.S. Forest Service.
- Keesing, F., R.D. Holt, and R.S. Ostfeld. 2006. Effects of species diversity on disease risk. *Ecology Letters* 9(4):485–498.
- Keesing, F., L.K. Belden, P. Daszak, A. Dobson, C.D. Harvell, R.D. Holt, P. Hudson, A. Jolles, K.E. Jones, C.E. Mitchell, S.S. Myers, T. Bogich, and R.S. Ostfeld. 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* 468(7324):647–652.
- Kegley, A. and R.A. Snieszko. 2004. Variation in blister rust resistance among 226 *Pinus monticola* and 217 *P. lambertiana* seedling families in the Pacific Northwest. Pp. 209–226 in *Breeding and Genetic Resources of*

- Five-needle Pines: Growth, Adaptability, and Pest Resistance, R.A. Snieszko, S. Samman, S.E. Schlarbaum, and H.B. Kriebel, eds. Fort Collins, CO: U.S. Forest Service.
- Kenis, M., B.P. Hurley, A.E. Hajek, and M.J. Cock. 2017. Classical biological control of insect pests of trees: Facts and figures. *Biological Invasions* 19(11):3401–3417.
- Kinloch, B.B., Jr., and G.E. Dupper. 2002. Genetic specificity in the white pine-blister rust pathosystem. *Phytopathology* 92(3):278–280.
- Kinloch, B.B., Jr., D. Burton, D.A. Davis, R.D. Westfall, J. Dunlap, and D. Vogler. 2012. Strong partial resistance to white pine blister rust in sugar pine. Pp. 80–91 in *Proceedings of the Fourth International Workshop on the Genetics of Host–Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees*, R.A. Snieszko, A.D. Yanchuk, J.T. Kliejunas, K.M. Palmieri, J.M. Alexander, and S.J. Frankel, tech. cords. Albany, CA: U.S. Forest Service.
- Kinloch, B.B., Jr., D.A. Davis and D. Burton. 2008. Resistance and virulence interactions between two white pine species and blister rust in a 30-year field trial. *Tree Genetics & Genomes* 4(1):65–74.
- Kinloch, B.B., Jr., R.A. Snieszko, and G.E. Dupper. 2004. Virulence gene distribution and dynamics of the white pine blister rust pathogen in western North America. *Phytopathology* 94(7):751–758.
- Klein, T.M., E.D. Wolf, R. Wu, and J.C. Sanford. 1987. High-velocity microprojectiles for delivering nucleic acids into living cells. *Nature* 327(6117):70–73.
- Knight, K.S., J.P. Brown, and R.P. Long. 2013. Factors affecting the survival of ash *Fraxinus* spp. trees infested by emerald ash borer *Agrilus planipennis*. *Biological Invasions* 15(2):371–383.
- Knight, K.S., D. Herms, R. Plumb, E. Sawyer, D. Spalink, E. Pisarczyk, B. Wiggin, R. Kappler, E. Ziegler, and K. Menard. 2012. Dynamics of surviving ash (*Fraxinus* spp.) populations in areas long infested by emerald ash borer (*Agrilus planipennis*). Pp. 143–152 in *Proceedings of the Fourth International Workshop on the Genetics of Host–Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees*, R.A. Snieszko, A.D. Yanchuk, J.T. Kliejunas, K.M. Palmieri, J.M. Alexander, and S.J. Frankel, tech. cords. Albany, CA: U.S. Forest Service.
- Koch, J.L., D.W. Carey, M.E. Mason, T.M. Poland, and K.S. Knight. 2015. Intraspecific variation in *Fraxinus pennsylvanica* responses to emerald ash borer (*Agrilus planipennis*). *New Forests* 46(5–6):995–1011.
- Kong, L., C.T. Holtz, C.J. Nairn, H. Houke, W.A. Powell, K. Baier, and S.A. Merkle. 2014. Application of airlift bioreactors to accelerate genetic transformation in American chestnut. *Plant Cell, Tissue and Organ Culture* 117(1):39–50.
- La, Y.-J. 2009. Korean successes in controlling blister rust of Korean pine. Pp. 1–9 in *Breeding and Genetic Resources of Five-Needle Pines Conference*, D. Noshad, E. Noh, J. King, and R. Snieszko, eds. Yangyang: Korea Forest Research Institute.
- Lane, T., T. Best, N. Zembower, J. Davitt, N. Henry, Y. Xu, J. Koch, H. Liang, J. McGraw, S. Schuster, D. Shim, M.V. Coggeshall, J.E. Carlson, and M.E. Staton. 2016. The green ash transcriptome and identification of genes responding to abiotic and biotic stresses. *BMC Genomics* 17:702.
- Langner, T., S. Kamoun, and K. Belhaj. 2018. CRISPR crops: Plant genome editing toward disease resistance. *Annual Review of Phytopathology* 56(1):479–512.
- Lattanzio, V., V.M. Lattanzio, and A. Cardinali. 2006. Role of phenolics in the resistance mechanisms of plants against fungal pathogens and insects. *Phytochemistry: Advances in Research* 66(2):23–67.
- LeBoldus, J.M., P.V. Blenis, and B.R. Thomas. 2010. A method to induce stem cankers by inoculating nonwounded populus clones with *Septoria musiva* spore suspensions. *Plant Disease* 94(10):1238–1242.
- LeBoldus, J.M., P. Blenis, B.R. Thomas, N. Feau, and L. Bernier. 2009. Susceptibility of *Populus balsamifera* to *Septoria musiva*: A field study and greenhouse experiment. *Plant Disease* 93(11):1146–1150.
- LeBoldus, J.M., N. Isabel, K.D. Floate, P. Blenis, and B. R. Thomas. 2013. Testing the “hybrid susceptibility” and “phenological sink” hypotheses using the *P. balsamifera*–*P. deltoides* hybrid zone and *Septoria* leaf spot [*Septoria musiva*]. *PLoS ONE* 8(12):e84437.
- Lee, J.H., and P.M. Pijut. 2017. Adventitious shoot regeneration from in vitro leaf explants of *Fraxinus nigra*. *Plant Cell, Tissue and Organ Culture* 130(2):335–343.
- Leimu, R., and J. Koricheva. 2006. A meta-analysis of tradeoffs between plant tolerance and resistance to herbivores: Combining the evidence from ecological and agricultural studies. *Oikos* 112(1):1–9.
- Leung, B., M.R. Springborn, J.A. Turner, and E.G. Brockhoff. 2014. Pathway-level risk analysis: The net present value of an invasive species policy in the US. *Frontiers in Ecology and the Environment* 12(5):273–279.
- Li, D., J. Zhang, and S.A. Merkle. 2014. Induction of green ash embryonic cultures with potential for scalable somatic embryo production using suspension culture. *Trees* 28(1):253–262.

- Liang, H., C.M. Catranis, C.A. Maynard, and W.A. Powell. 2002. Enhanced resistance to the poplar fungal pathogen, *Septoria musiva*, in hybrid poplar clones transformed with genes encoding antimicrobial peptides. *Biotechnology Letters* 24(5):383–389.
- Liang, H., C.A. Maynard, R.D. Allen, and W.A. Powell. 2001. Increased *Septoria musiva* resistance in transgenic hybrid poplar leaves expressing a wheat oxalate oxidase gene. *Plant Molecular Biology* 45(6):619–629.
- Liang, H., M. Staton, Y. Xu, T. Xu, and J. Leboldus. 2014. Comparative expression analysis of resistant and susceptible *Populus* clones inoculated with *Septoria musiva*. *Plant Science* 223:69–78.
- Liebholt, A.M., E.G. Brockerhoff, S. Kalisz, M.A. Nuñez, D.A. Wardle, and M.J. Wingfield. 2017. Biological invasions in forest ecosystems. *Biological Invasions* 19(11):3437–3458.
- Liebholt, A.M., L. Berec, E.G. Brockerhoff, R.S. Epanchin-Niell, A. Hastings, D.A. Herms, J.M. Kean, D.G. McCullough, D.M. Suckling, P.C. Tobin, and T. Yamanaka. 2016. Eradication of invading insect populations: From concepts to applications. *Annual Review of Entomology* 61:335–352.
- Liu, Y.-C., M.L. Double, W.L. MacDonald, and M.G. Milgroom. 2002. Persistence of *Cryphonectria hypoviruses* after their release for biological control of chestnut blight in West Virginia forests. *Forest Pathology* 32(6):345–356.
- Liu, Y.-C., and M.G. Milgroom. 1996. Correlation between hypovirus transmission and the number of vegetative incompatibility (*vic*) genes different among isolates from a natural population of *Cryphonectria parasitica*. *Phytopathology* 86(1):79–86.
- Lovett, G.M., M. Weiss, A.M. Liebhold, T.P. Holmes, B. Leung, K.F. Lambert, D.A. Orwig, F.T. Campbell, J. Rosenthal, D.G. McCullough, R. Wildova, M.P. Ayres, C.D. Canham, D.R. Foster, S.L. LaDeau, and T. Weldy. 2016. Nonnative forest insects and pathogens in the United States: Impacts and policy options. *Ecological Applications* 26(5):1437–1455.
- Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, M. and F.A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10(3):689–710.
- Maher, C.T., C.R. Nelson, A.J. Larson, and A. Sala. 2018. Ecological effects and effectiveness of silvicultural restoration treatments in whitebark pine forests. *Forest Ecology and Management* 429:534–548.
- Maloy, O.C. 1997. White pine blister rust control in North America: A case history. *Annual Review of Phytopathology* 35:87–109.
- Margoless, D.S. 2011. Mountain Pine Beetle–Whitebark Pine Dynamics in a Subalpine Ecosystem of the Pioneer Mountains, Southwest Montana. Master (M.S.) Thesis, University of Minnesota.
- Martín-Trillo, M., and J.M. Martínez-Zapater. 2002. Growing up fast: Manipulating the generation time of trees. *Current Opinion in Biotechnology* 13(2):151–155.
- Maxwell, D.L., E.L. Kruger, and G.R. Stanosz. 1997. Effects of water stress on colonization of poplar stems and excised leaf disks by *Septoria musiva*. *Phytopathology* 87(4):381–388.
- McCullough, D.G., and R.J. Mercader. 2012. Evaluation of potential strategies to SLOW Ash Mortality (SLAM) caused by emerald ash borer (*Agilus planipennis*): SLAM in an urban forest. *International Journal of Pest Management* 58(1):9–23.
- McCullough, D.G., R.J. Mercader, and N.W. Siegert. 2015. Developing and integrating tactics to slow ash (Oleaceae) mortality caused by emerald ash borer (Coleoptera: Buprestidae). *The Canadian Entomologist* 147(3):349–358.
- McDonald, B.A., and C. Linde. 2002. Pathogen population genetics, evolutionary potential and durable resistance. *Annual Review of Phytopathology* 40:349–379.
- McDonald, G., P. Zambino, and R. Sniezko. 2004. Breeding rust-resistant five-needle pines in the western United States. Pp. 28–50 in *Breeding and Genetic Resources of Five-needle Pines: Growth, Adaptability, and Pest Resistance*, R.A. Sniezko, S. Samman, S.E. Schlarbaum, and H.B. Kriebel, eds. Fort Collins, CO: U.S. Forest Service.
- McKinney, S.T., and D.F. Tomback. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. *Canadian Journal of Forest Research* 37(6):1044–1057.
- Mercader, R.J., D.G. McCullough, A.J. Storer, J.M. Bedford, R. Heyd, N.W. Siegert, S. Katovich, and T.M. Poland. 2016. Estimating local spread of recently established emerald ash borer, *Agilus planipennis*, infestations and the potential to influence it with a systemic insecticide and girdled ash trees. *Forest Ecology and Management* 366:87–97.
- Mercader, R.J., N.W. Siegert, A.M. Liebhold, and D.G. McCullough. 2011. Simulating the effectiveness of three potential management options to slow the spread of emerald ash borer (*Agilus planipennis*) populations in localized outlier sites. *Canadian Journal of Forest Research* 41(2):254–264.
- Merkle, S.A., and J.F.D. Dean. 2000. Forest tree biotechnology. *Current Opinion in Biotechnology* 11(3):298–302.

- Merkle, S.A., A.R. Tull, H.J. Gladfelter, P.M. Montello, J.E. Mitchell, C. Ahn, and R.D. McNeill. 2017. Somatic embryogenesis and cryostorage for conservation and restoration of threatened forest trees. Pp. 113–116 in Proceedings of Workshop on Gene Conservation of Tree Species–Banking on the Future, R.A. Snieszko, G. Man, V. Hipkins, K. Woeste, D. Gwaze, J.T.Kliejunas, and B.A. McTeague, tech. coords. Portland, OR: USDA–FS.
- Merkle, S.A., A.T. Wiecko, and A.B. Watson-Pauley. 1991. Somatic embryogenesis in American chestnut. Canadian Journal of Forest Research 21(11):1698–1701.
- Milgroom, M.G., and P. Cortesi. 2004. Biological control of chestnut blight with hypovirulence: A critical analysis. Annual Review of Phytopathology 42:311–338.
- Mundt, C.C., 2014. Durable resistance: A key to sustainable management of pathogens and pests. Infection, Genetics and Evolution 27:446–455.
- NASEM (National Academies of Sciences, Engineering, and Medicine). 2016. Gene Drives on the Horizon: Advancing Science, Navigating Uncertainty, and Aligning Research with Public Values. Washington, DC: The National Academies Press.
- Neuhaus, G., and G. Spangenberg. 1990. Plant transformation by microinjection techniques. Physiologia Plantarum 79(1):213–217.
- Newcombe, G., and M. Ostry. 2001. Recessive resistance to Septoria stem canker of hybrid poplar. Phytopathology 91(11):1081–1084.
- Newhouse, A. 2018. Transgenic American Chestnuts for Potential Forest Restoration: Scientific Successes, Regulatory Challenges. Presentation at the Genetic Engineering and Society Center Colloquium, April 24, North Carolina State University, Raleigh, NC. Available at <https://research.ncsu.edu/ges/colloquium/2017-18-colloquial/>. Accessed November 27, 2018.
- Newhouse, A.E., L.D. McGuigan, K.A. Baier, K.E. Valletta, W.H. Rottmann, T.J. Tschaplinski, C.A. Maynard, and W.A. Powell. 2014a. Transgenic American chestnuts show enhanced blight resistance and transmit the trait to T1 progeny. Plant Science 228:88–97.
- Newhouse, A.E., J.E. Spitzer, C.A. Maynard, and W.A. Powell. 2014b. Chestnut leaf inoculation assay as a rapid predictor of blight susceptibility. Plant Disease 98(1):4–9.
- Nguyen, V.P., J.-S. Cho, J.-H. Lee, M.-H. Kim, Y.-I. Choi, E.-J. Park, W.-C. Kim, S. Hwang, K.-H. Han, and J.-H. Ko. 2017. Identification and functional analysis of a promoter sequence for phloem tissue specific gene expression from *Populus trichocarpa*. Journal of Plant Biology 60(2):129–136.
- Ostry, M.E. 1987. Biology of Septoria musiva and Marssonina brunnea in hybrid Populus plantations and control of Septoria canker in nurseries. European Journal of Forest Pathology 17(3):158–165.
- Ostry, M.E., G. Laflamme, and S.A. Katovich. 2010. Silvicultural approaches for management of eastern white pine to minimize impacts of damaging agents. Forest Pathology 40(3–4): 332–346.
- Ostry, M.E., and K.T. Ward. 2003. Field performance of *Populus* expressing somaclonal variation in resistance to *Septoria musiva*. Plant Science 164(1):1–8.
- Padovan, A., A. Keszeci, W.J. Foley and C. Külheim. 2013. Differences in gene expression with a striking phenotypic mosaic *Eucalyptus* tree that varies in susceptibility to herbivory. BMC Plant Biology 13:29.
- Palla, K.J., and P.M. Pijut. 2015. *Agrobacterium*-mediated genetic transformation of *Fraxinus americana* hypocotyls. Plant Cell, Tissue and Organ Culture 120(2):631–641.
- Palloix, A., V. Ayme, and B. Moury. 2009. Durability of plant major resistance genes to pathogens depends on the genetic background, experimental evidence and consequences for breeding strategies. New Phytologist 183(1): 190–199.
- Parlevliet, J.E., and J.C. Zadoks. 1977. The integrated concept of disease resistance: A new view including horizontal and vertical resistance in plants. Euphytica 26(1):5–21.
- Perkins, D.L., C.L. Jorgensen, and M.J. Rinella. 2015. Verbenone decreases whitebark pine mortality throughout a mountain pine beetle outbreak. Forest Science 61(4):747–752.
- Pickett, C.H., J.C. Ball, K.C. Casanave, K.M. Klonsky, K.M. Jetter, L.G. Bezark, and S.E. Schoenig. 1996. Establishment of the ash whitefly parasitoid *Encarsia inaron* (Walker) and its economic benefit to ornamental street trees in California. Biological Control 6(2):260–272.
- Plomion, C., J.-M. Aury, J. Amselem, T. Leroy, F. Murat, S. Duplessis, S. Faye, N. Francillonne, K. Labadie, G. Le Provost, I. Lesur, J. Bartholomé, P. Faivre-Rampant, A. Kohler, J.-C. Leplé, N. Chantret, J. Chen, A. Diévert, T. Alaeitabar, V. Barbe, C. Belser, H. Bergès, C. Bodénès, M.-B. Bogeat-Triboulot, M.-L. Bouffaud, B. Brachi, E. Chancerel, D. Cohen, A. Couloux, C. Da Silva, C. Dossat, F. Ehrenmann, C. Gaspin, J. Grima-Pettenati, E. Guichoux, A. Hecker, S. Herrmann, P. Hugueney, I. Hummel, C. Klopp, C. Lalanne, M. Lascoux, E. Lasserre, A. Lemainque, M.-L. Desprez-Loustau, I. Luyten, M.-A. Madoui, S. Mangenot, C. Marchal, F. Maumus, J.

- Mercier, C. Michotey, O. Panaud, N. Picault, N. Rouhier, O. Rué, C. Rustenholz, F. Salin, M. Soler, M. Tarkka, A. Velt, A.E. Zanne, F. Martin, P. Wincker, H. Quesneville, A. Kremer, and J. Salse. 2018. Oak genome reveals facets of long lifespan. *Nature Plants* 4 (7): 440–452.
- Poland, T.M., and D.G. McCullough. 2006. Emerald ash borer: Invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry* 104(3):118–124.
- Polin, L.D., H. Liang, R.E. Rothrock, M. Nishii, D.L. Diehl, A.E. Newhouse, C.J. Nairn, W.A. Powell, and C.A. Maynard. 2006. *Agrobacterium*-mediated transformation of American chestnut (*Castanea dentata* (Marsh.) Borkh.) somatic embryos. *Plant Cell, Tissue and Organ Culture* 84(1):69–79.
- Powell W.A. 2014. The American chestnut's genetic rebirth. *Scientific American* 310:68–73.
- Prasad, A.M., L.R. Iverson, M.P. Peters, J.M. Bossenbroek, S.N. Matthews, S.D. Syndor, and M.W. Schwartz. 2010. Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. *Landscape Ecology* 25(3):353–369.
- Qin, R., and J.M. LeBoldus. 2014. The infection biology of *Sphaerulina musiva*: Clues to understanding a forest pathogen. *PLoS ONE* 9(7):e103477.
- Raffa, K.F., B.H. Aukema, B.J. Bentz, A.L. Carroll, J.A. Hicke, M.G. Turner, and W.H. Romme. 2008. Cross-scale drivers of natural disturbance prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *Bioscience* 58(6):501–517.
- Raffa, K.F., E.N. Powell, and P.A. Townsend. 2013. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proceedings of the National Academy of Sciences of the United States of America* 110(6):2193–2198.
- Rasche, L., L. Fahse, and H. Bugmann. 2013. Key factors affecting the future provision of tree-based forest ecosystem goods and services. *Climatic change* 118(3–4):579–593.
- Remington, D.L., and D.M. O'Malley. 2000. Whole-genome characterization of embryonic stage inbreeding depression in a selfed loblolly pine family. *Genetics* 155(1):337–348.
- Resende, M.F.R., P. Muñoz, J.J. Acosta, G.F. Peter, J.M. Davis, D. Grattapaglia, M.D.V. Resende, and M. Kirst. 2012. Accelerating the domestication of trees using genomic selection: Accuracy of prediction models across ages and environments. *New Phytologist* 193(3):617–624.
- Rigsby, C.M., D.A. Herms, P. Bonello, and D. Cipollini. 2016. Higher activities of defense-associated enzymes may contribute to greater resistance of Manchurian ash to emerald ash borer than a closely related and susceptible congener. *Journal of Chemical Ecology* 42(8):782–792.
- Riyal, D. 2011. Development of Mutation Based Breeding Technology in Forest Tree Species. M.S. thesis, Simon Fraser University.
- Rose, R. 2018. USDA, Animal and Plant Health Inspection Service, Plant Protection and Quarantine: Biological control permitting overview. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, February 23.
- Roy, B.A., H.M. Alexander, J. Davidson, F.T. Campbell, J.J. Burdon, R. Sniezko, and C. Brasier. 2014. Increasing forest loss worldwide from invasive pests requires new trade regulations. *Frontiers in Ecology and the Environment* 12(8):457–465.
- Sanford, J.C., T.M. Klein, E.D. Wolf, and N. Allen. 1987. Delivery of substances into cells and tissues using a particle bombardment process. *Particulate Science and Technology* 5(1):27–37.
- Santos, C., H. Machado, I. Correia, F. Gomes, J. Gomes-Laranjo, and R. Costa. 2015. Phenotyping *Castanea* hybrids for *Phytophthora cinnamomi* resistance. *Plant Pathology* 64(4):901–910.
- Schoenweiss, K., and A. Meier-Dinkel. 2005. *In vitro* propagation of selected mature trees and juvenile embryo-derived cultures of common ash (*Fraxinus excelsior* L.). *Propagation of Ornamental Plants* 5(3):137–145.
- Schwandt, J.W., I.B. Lockman, J.T. Kliejunas, and J.A. Muir. 2010. Current health issues and management strategies for white pines in the western United States and Canada. *Forest Pathology* 40(3–4):226–250.
- Sharov, A.A., D. Leonard, A.M. Liebhold, E.A. Roberts, and W. Dickerson. 2002. "Slow the spread": A national program to contain the gypsy moth. *Journal of Forestry* 100(5):30–36.
- Shelton, A.M., J. Zhao, and R.T. Roush. 2002. Economic, ecological, food safety, and social consequences of the deployment of Bt transgenic plants. *Annual Reviews in Entomology* 47:845–881.
- Showalter, D.N., K.F. Raffa, R.A. Sniezko, D.A. Herms, A.M. Liebhold, J.A. Smith, and P. Bonello. 2018. Strategic development of tree resistance against forest pathogen and insect invasions in defense-free space. *Frontiers in Ecology and Evolution* 6:124.
- Simmonds, N. 1991. Genetics of horizontal resistance to diseases of crops. *Biological Reviews* 66(2):189–241.
- Sisco, P.H. 2004. Breeding blight resistant American chestnut trees. *Journal of The American Chestnut Foundation* 18:15.

- Six, D.L., C. Vergobbi, and M. Cutter. 2018. Are survivors different? Genetic-based selection of trees by mountain pine beetle during a climate change-driven outbreak in a high-elevation pine forest. *Frontiers in Plant Science* 9:993.
- Snieszko, R.A., and J. Koch. 2017. Breeding trees resistant to insects and diseases: Putting theory into application. *Biological Invasions* 19(11):3377–3400.
- Snieszko, R.A., A. Bower, and J. Danielson. 2000. A comparison of early field results of white pine blister rust resistance in sugar pine and western white pine. *HortTechnology* 10(3):519–522.
- Snieszko, R.A., A. Kegley, R. Danchok, and S. Long. 2007. Variation in resistance to white pine blister rust among whitebark pine families from Oregon and Washington—early results and implications for conservation. Pp. 82–97 in *Proceedings of the Conference Whitebark Pine: A Pacific Coast Perspective*, E.M. Goheen and R.A. Snieszko, tech. cords. Portland, OR: U.S. Forest Service.
- Snieszko, R.A., A. Kegley, R. Danchok, and S. Long. 2018. Blister rust resistance in whitebark pine (*Pinus albicaulis*)—early results following artificial inoculation of seedlings from Oregon, Washington, Idaho, Montana, California, and British Columbia seed sources. Pp. 129–135 in *Proceedings of the IUFRO Joint Conference: Genetics of Five-needle Pines, Rusts of Forest Trees, and Strobosphere*, A.W. Schoettle, R.A. Snieszko, and J.T. Kliejunas, eds. Fort Collins, CO: U.S. Forest Service.
- Snieszko, R.A., J. Hamlin, and E.M. Hansen. 2012. Operational program to develop *Phytophthora lateralis*-resistant populations of Port-Orford-cedar (*Chamaecyparis lawsoniana*). Pp. 65–79 in *Proceedings of the Fourth International Workshop on the Genetics of Host–Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees*, R.A. Snieszko, A.D. Yanchuk, J.T. Kliejunas, K.M. Palmieri, J.M. Alexander, and S.J. Frankel, tech. cords. Albany, CA: U.S. Forest Service.
- Snieszko, R.A., M.F. Mahalovich, A.W. Schoettle, and D.R. Vogler. 2011. Past and current investigations of the genetic resistance to *Cronartium ribicola* in high-elevation five-needle pines. Pp. 246–264 in *The Future of High-elevation, Five-needle White Pines in Western North America: Proceedings of the High Five Symposium*, R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith, eds. Fort Collins, CO: U.S. Forest Service.
- Snieszko, R.A., J. Smith, J.-J. Liu, and R.C. Hamelin. 2014. Genetic resistance to fusiform rust in southern pines and white pine blister rust in white pines—A contrasting tale of two rust pathosystems—Current status and future prospects. *Forests* 5(9):2050–2083.
- Sollars, E.S.A., A.L. Harper, L.J. Kelly, C.M. Sambles, R.H. Ramirez-Gonzalez, D. Swarbreck, G. Kaithakottil, E.D. Cooper, C. Uauy, L. Havlickova, G. Worswick, D.J. Studholme, J. Zohren, D. L. Salmon, B.J. Clavijo, Y. Li, Z. He A. Fellgett, L.V. McKinney, L.R. Nielsen, G.C. Douglas, E.D. Kjær, J.A. Downie, D. Boshier, S. Lee, J. Clark, M. Grant, I. Bancroft, M. Caccamo, R.J.A. Buggs. 2017. Genome sequence and genetic diversity of European ash trees. *Nature* 541(7636):212–216.
- Springer, P.S. 2000. Gene traps: Tools for plant development and genomics. *Plant Cell* 12(7):1007–1020.
- Steiner, K.C., J.W. Westbrook, F.V. Hebard, L.L. Georgi, W.A. Powell, and S.F. Fitzsimmons S.F. 2017. Rescue of American chestnut with extraspecific genes following its destruction by a naturalized pathogen. *New Forests* 48(2):317–336.
- Stevens, M.E., and P.M. Pijut. 2014. *Agrobacterium*-mediated genetic transformation and plant regeneration of the hardwood tree species *Fraxinus profunda*. *Plant Cell Reports* 33(6):861–870.
- Stevens, K.A., J.L. Wegrzyn, A. Zimin, D. Puiu, M. Crepeau, C. Cardeno, R. Paul, D. Gonzalez-Ibeas, M. Koriabine, A.E. Holtz-Morris, P.J. Martínez-García, U.U. Sezen, G. Marçais, K. Jermstad, P.E. McGuire, C.A. Loopstra, J.M. Davis, A. Eckert, P. de Jong, J.A. Yorke, S.L. Salzberg, D.B. Neale, and C.H. Langley. 2016. Sequence of the sugar pine megagenome. *Genetics* 204(4):1613–1626.
- Stoddard, E.M., and A.E. Moss. 1913. *The Chestnut Bark Disease*, Bulletin 178. New Haven: The Connecticut Agricultural Experiment Station.
- Suprasanna, P., T.R. Ganapathi, and V.A. Bapat. 2005. Genetic transformation of woody plants using embryogenic cultures. *Journal of New Seeds* 7(2):17–35.
- Tang, G., B.J. Reinhart, D.P. Bartel, and P.D. Zamore. 2003. A biochemical framework for RNA silencing in plants. *Genes & Development* 17(1):49–63.
- Telford, A., S. Cavers, R.A. Ennos, and J.E. Cottrell. 2015. Can we protect forests by harnessing variation in resistance to pests and pathogens? *Forestry* 88(1):3–12.
- Thynne, E., I.M.L. Saur, J. Simbaqueba, H.A. Ogilvie, Y. Gonzalez-Cendales, O. Mead, A. Taranto, A.-M. Catanzariti, M.C. McDonald, B. Schwessinger, D.A. Jones, J.P. Rathjen, and P.S. Solomon. 2017. Fungal phytopathogens encode functional homologues of plant rapid alkalization factor (RALF) peptides. *Molecular Plant Pathology* 18(6):811–824.

- Tobin, P.C., J.M. Kean, D.M. Suckling, D.G. McCullough, D.A. Herms, and L.D. Stringer. 2014. Determinants of successful arthropod eradication programs. *Biological Invasions* 16(2):401–414.
- Tomback, D.F., A.J. Anderies, K.S. Carsey, M.I. Powell, and S. Mellman-Brown. 2001. Delayed seed germination in whitebark pine and regeneration pattern following the Yellowstone fires. *Ecology* 82(9): 2587–2600.
- Tsai, C.J., and L.J. Xue. 2015. CRISPRing into the woods. *GM Crops & Food* 6(4):206–215.
- Tscharntke, T., R. Bommarco, Y. Clough, T.O. Crist, D. Kleijn, T.A. Rand, J.M. Tylianakis, J.M., S. van Nouhuys, and S. Vidal. 2008. Reprint of “Conservation biological control and enemy diversity on a landscape scale” [Biol. Control 43 (2007) 294–309]. *Biological Control* 45(2):238–253.
- Tuskan, G.A., S. DiFazio, S. Jansson, J. Bohlmann, I. Grigoriev, U. Hellsten, N. Putnam, S. Ralph, S. Rombauts, A. Salamov, J. Schein, L. Sterck, A. Aerts, R.R. Bhalerao, R.P. Bhalerao, D. Blaudez, W. Boerjan, A. Brun, A. Brunner, V. Busov, M. Campbell, J. Carlson, M. Chalot, J. Chapman, G.-L. Chen, D. Cooper, P.M. Coutinho, J. Couturier, S. Covert, Q. Cronk, R. Cunningham, J. Davis, S. Degroove, A. Déjardin, C. dePamphilis, J. Detter, B. Dirks, I. Dubchak, S. Duiplessis, J. Ehlting, B. Ellis, K. Gendler, D. Goodstein, M. Gribskov, J. Grimwood, A. Groover, L. Gunter, B. Hamberger, B. Heinze, Y. Helariutta, B. Henrissat, D. Holligan, R. Holt, W. Huang, N. Islam-Faridi, S. Jones, M. Jones-Rhoades, R. Jorgensen, C. Joshi, J. Kangasjärvi, J. Karlsson, C. Kelleher, R. Kirkpatrick, M. Kirst, A. Kohler, U. Kalluri, F. Larimer, J. Leebens-Mack, J.-C. Leplé, P. Locascio, Y. Lou, S. Lucas, F. Martin, B. Montanini, C. Napoli, D.R. Nelson, C. Nelson, K. Nieminen, O. Nilsson, V. Pereda, G. Peter, R. Philippe, G. Pilate, A. Poliakov, J. Razumovskaya, P. Richardson, C. Rinaldi, K. Ritland, P. Rouzé, D. Ryaboy, J. Schmutz, J. Schrader, B. Segerman, H. Shin, A. Siddiqui, F. Sterkyk, A. Terry, C.-J. Tsai, E. Uberbacher, P. Unneberg, J. Vahala, K. Wall, S. Wessler, G. Yang, T. Yin, C. Douglas, M. Marra, G. Sandberg, Y. Van de Peer, and D. Rokhsar. 2006. The genome of black cottonwood, *Populus trichocarpa* (Torr. & Gray). *Science* 313(5793):1596–1604.
- Tuzun, S. 2001. The relationship between pathogen-induced systemic resistance (ISR) and multigenic (horizontal) resistance in plants. *European Journal of Plant Pathology* 107(1):85–93.
- USDA-APHIS (U.S. Department of Agriculture Animal and Plant Health Inspection Service). 2007. Availability of an Environmental Assessment for the Proposed Release of Three Parasitoids for the Biological Control of the Emerald Ash Borer *Agilus planipennis* in the Continental United States. Federal Register 72:28947–28948.
- Venette, R.C., D.J. Kriticos, R.D. Magarey, F.H. Koch, R.H. Baker, S.P. Worner, N.N. Gómez Raboteaux, D.W. McKenney, E.J. Dobesberger, D. Yemshanov, and P.J. De Barro. 2010. Pest risk maps for invasive alien species: a roadmap for improvement. *BioScience* 60(5):349–362.
- Wainhouse, D. 2005. *Ecological Methods in Forest Pest Management*. Oxford: Oxford University Press.
- Wang, H., M. La Russa, and L.S. Qi. 2016. CRISPR/cas9 in genome editing and beyond. *Annual Review of Biochemistry* 85(1):227–264.
- Welch, A.J., A.J. Stipanovic, C.A. Maynard, and W.A. Powell. 2007. The effects of oxalic acid on transgenic *Castanea dentata* callus tissue expressing oxalate oxidase. *Plant Science* 172(3):488–496.
- Westbrook, J. 2017. Restoration of American chestnut: A marriage of breeding and biotechnology. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, December 12.
- Westbrook, J.W., J.B. James, S. Lucas, F.V. Hebard, J. Frampton, and S.N. Jeffers. 2018. Resistance to *Phytophthora cinnamomi* in American chestnut (*Castanea dentata*) backcross populations that descended from two Chinese chestnut (*Castanea mollissima*) sources of resistance. *Plant Disease* forthcoming.
- White, T.L., W.T. Adams, and D.B. Neale. 2007. *Forest Genetics*. Cambridge, MA: CABI.
- Whitehill, J.G.A., S.O. Opiyo, J.L. Koch, D.A. Herms, D.F. Cipollini, and P. Bonello. 2012. Interspecific comparison of constitutive ash phloem phenolic chemistry reveals compounds unique to Manchurian ash, a species resistant to emerald ash borer. *Journal of Chemical Ecology* 38(5):499–511.
- Williams, C., R.D. Barnes, and I. Nyoka. 1999. Embryonic genetic load for a neotropical conifer, *Pinus patula* Schiede et Deppe. *Journal of Heredity* 90(3):394–398.
- Woodbury, P.B., J.A. Laurence, and G.W. Hudler. 1994. Chronic ozone exposure increases the susceptibility of hybrid *Populus* to disease caused by *Septoria musiva*. *Environmental Pollution* 86(1):109–114.
- Woodcock, P, J.E. Cottrell, R.J.A. Buggs, and C.P. Quine. 2017. Mitigating pest and pathogen impacts using resistant trees: A framework and overview to inform development and deployment in Europe and North America. *Forestry* 91(1):1–16.
- Wu, S.H., S.X. Zhang, J.Q. Chao, X.M. Deng, Y.Y. Chen, M.J. Shi, and W.M. Tian. 2016. Transcriptome analysis of the signalling networks in coronatine-induced secondary laticifer differentiation from vascular cambia in rubber trees. *Scientific Reports* 6:36384.

- Yang, D., L. Bernier, and M. Dessureault. 1994. Biological control of Septoria leaf spot of poplar by *Phaeotheca dimorphospora*. *Plant Disease* 78(8):821–825.
- Zayed, M.Z., W.-S. Ho, S.-L. Pang, and F.B. Ahmad 2014. EMS-induced mutagenesis and DNA polymorphism assessment through ISSR markers in *Neolamarckia cadamba* (kelampayan) and *Leucaena leucocephala* (petai belalang). *European Journal of Experimental Biology* 4(4):156–163.
- Zhang, B., A. Newhouse, L. McGuigan, C. Maynard, and W. Powell. 2011. Agrobacterium-mediated co-transformation of American chestnut (*Castanea dentata*) somatic embryos with a wheat oxalate oxidase gene. *BMC Proceedings* 5(Suppl 7):O43.
- Zhang, B., A.D. Oakes, A.E. Newhouse, K.M. Baier, C.A. Maynard and W.A. Powell. 2013. A threshold level of oxalate oxidase transgene expression reduces *Cryphonectria parasitica*-induced necrosis in a transgenic American chestnut (*Castanea dentata*) leaf bioassay. *Transgenic Research* 22(5):973–982.
- Zhang, D.-X., M.J. Spiering, A.L. Dawe, and D.L. Nuss. 2014. Vegetative incompatibility loci with dedicated roles in allorecognition restrict mycovirus transmission in chestnut blight fungus. *Genetics* 197(2):701–714.
- Zhang, D.-X., and D.L. Nuss. 2016. Engineering super mycovirus donor strains of chestnut blight fungus by systematic disruption of multilocus *vic* gene. *Proceedings of the National Academy of Sciences of the United States of America* 113:2062–2067.
- Zhang, X.Y., Q. Lu, R.A. Snieszko, R.Q. Song, and G. Man. 2010. Blister rusts in China: Hosts, pathogens, and management. *Forest Pathology* 40(3–4):369–381.
- Zimin, A., K.A. Stevens, M.W. Crepeau, A. Holtz-Morris, M. Koriabine, G. Marçais, D. Puiu, M. Roberts, J.L. Wegrzyn, P.J. de Jong, D.B. Neale, S.L. Salzberg, J.A. Yorke, and C.H. Langley. 2014. Sequencing and assembly of the 22-gb loblolly pine genome. *Genetics* 196(3):875–890.
- Zupan, J.R., and P. Zambryski. 1995. Transfer of T-DNA from Agrobacterium to the plant cell. *Plant Physiology* 107(4):1041–1047.

Ecological, Economic, Social, and Ethical Considerations in the Use of Biotechnology in Forest Trees

Any intervention to address forest health involves consideration of associated ecological, economic, social, and ethical issues. This chapter discusses these considerations related to using biotechnology to mitigate forest health threats. Some of these considerations are unique to biotechnology, but others are applicable to any intervention.

ECOLOGICAL CONSIDERATIONS

From an ecological standpoint, the use of biotechnology to improve forest health is fundamentally different from a decision to employ biotechnology for pharmaceutical or other existing human uses, including (to some degree) crops. A general principle for these other biotechnological products is that the intent is for them to remain confined to the production site. Pharmaceutical products can generally be produced in a laboratory or industrial setting and thus kept secure from the broader environment. Most crops (biotech and nonbiotech) have been bred to grow in monocultures that are planted and harvested on an annual basis, and many of the plantings involve a single genotype. Although gene flow from crops is possible, escapes and hybridization with wild relatives are generally low (NASEM, 2016b). Conversely, in cases where biotechnological approaches are implemented to address forest health, the intention is to maximize spread of the modified genome into forests to confer increased genetic resistance to insect pests or pathogens throughout the range of the tree species. Furthermore, forest trees are perennials that grow and interact with many other species throughout their long life span.

The 2016 National Academies report on gene drives (NASEM, 2016a) identified several interacting factors that influence the success of a gene drive propagating in the environment, which has parallels to the spread of biotech trees for forest health (NASEM, 2016a:3)¹:

- The evolutionary “fitness” of individuals carrying the [genetic modification]—that is, their ability to produce fertile offspring—as compared to individuals not carrying the [genetic modification].
- The “conversion rate,” which describes how the [genetic modification] is passed to subsequent generations when one parent carries the [genetic modification] and the other does not.
- “Gene flow,” which describes how the [genetic modification] moves between different populations of the target species.
- “Horizontal gene transfer,” or the potential for [genetic modifications] to move from the target species into entirely different species.

For trees, the committee considers it important to add additional items to this list:

- Establishment, which describes the ability of individuals carrying the genetic modification to compete with other individuals, allowing establishment and growth to reproductive maturity.
- Standing genetic variation, which is the presence of alternative forms of a gene in a population.

¹The committee has replaced “gene drive” with “genetic modification.”

Furthermore, the report on gene drives noted that ecological factors at the community level are important to consider. These include a species' role in its community. Another factor to consider is the ability of a change to the species to create a tipping point from one ecological community configuration to another configuration. Genetic changes introduced into trees to address forest health threats have the potential to take on characteristics of invasive species that tip the balance of ecosystems.

Fitness and Conversion Rate

Attention to fitness and conversion rate will be critical because the intent of biotech trees would be to recover species over both large temporal and spatial scales ((Newhouse et al., 2014). Even substantial out-planting efforts will provide only founding individuals intended to result in populations with increased resistance to the insect pest or pathogen involved. These trees will have to retain “fitness” to survive and “convert” that fitness, that is, produce viable propagules with the resistance in future generations. To ensure genetic fitness over the long term, the possibility of trade-offs between genetic traits needs to be examined, that is, whether modifying plants for resistance results in trade-offs in growth, drought resistance, or seed production (Lovett, 2018). Given that forest trees will be on the landscape for decades to centuries, the conversion rate of any genetic resistance will have to provide durable and heritable resistance under unmanaged or minimally managed conditions over time (Sniezko and Koch, 2017). Certain types of resistance may have limited or no utility if they cannot be sustained in the population (Kinloch et al., 2004; Sniezko and Koch, 2017).

Gene Flow and Horizontal Gene Transfer

Many of the tree species under consideration are wind-pollinated, suggesting the potential for long-distance gene flow within the target species (Liepelt et al., 2002; Van Deynze et al., 2016; Semizer-Cuming et al., 2017). Furthermore, the possibility of long-distance pollen dispersal has been considered a potential evolutionary mechanism for tree populations to withstand the negative effects of climate change (Kremer et al., 2012). Thus, the confinement of gene flow (i.e., based on jurisdictional or cultural boundaries) would not be possible or even desired because presumably the trees with resistance will be the progenitors of future generations of the species. Additionally, interspecies gene flow, via horizontal gene transfer or hybridization, could also occur. Although the extent of horizontal gene transfer in plants is not well understood (Richardson and Palmer, 2007), several mechanisms of gene transfer between plant species have been described. Direct transfers can occur via parasitism, symbiosis, pathogens, epiphytes, entophyte, and grafting, and indirect mechanisms of horizontal gene transfer include pollen, fungi, bacteria, viruses, viroids, plasmids, transposons, and insects (see Gao et al., 2014, for a review). Even if the extent of horizontal gene transfer in plants is not well defined, hybridization between related plant species is common (Arnold, 1992). In the case of an introduced biotech tree, if hybridization with other species occurs, constraining such hybridization would be impossible unless hybrids had significantly reduced fitness (e.g., Ellstrand, 1992; Feurtey et al., 2017). Given that the tree species under consideration for this examination of biotechnology use on forest health are native species and that the introduced gene will likely spread within the native community, potential impacts both to the species involved and to the associated ecological and human communities need careful analysis (see section “Impact Assessment Framework” in Chapter 5; NASEM, 2016a).

Tree Establishment

For biotech trees to address forest health threats, they have to be competitive with their conspecifics and with other plant species in the ecosystem. Even if a biotech tree is genetically fit and able to convert its resistance to subsequent generations, it will not become established in a forest if it is not competitive in the ecosystem. This competitiveness needs to be balanced with any potential for the biotech tree to become a nuisance species, analogous to a nonnative invasive species that alters an ecosystem. Some characteristics

to consider when it comes to establishment are growth rate, maturation age, fecundity, root suckering, understory establishment, and allelopathy (Clark, 2018).

Role of Trees in Ecological Communities

By virtue of their woody growth, trees are able to develop perennial tissue that provides the structure for developing height and access to sunlight above other plants in the forest, making flowers more visible and accessible for pollination, generally via pollinators or wind, and dispersing seeds over long distances via wind, water, or animals. Woody stems support both dead and living tissues, providing important resources for multiple species across seasons and decades to centuries. As a result, forests harbor substantial biodiversity (Brockerhoff et al., 2017). Additionally, tree longevity means that biogeochemical cycles are locally influenced by trees, which stabilize soils and can alter local and regional climate (Bonan, 1999). Modeled impact of tree loss on carbon and nitrogen cycling suggests that some impacts may last for centuries (Crowley et al., 2016).

Disturbances of multiple scales in forests maintain successional gradients and biodiversity, recycle nutrients, and control population dynamics. Regional and local environmental variation have similar impacts. While pests have always had a natural role in individual, stand, and landscape dynamics of trees, the scale of that role has been substantially expanded with climate change, forest management, and pest introductions (see Chapter 2).

Exposure of trees to pest species over many generations has resulted in development of resistance to impacts of both specific and generalized pests. The distribution of this resistance may not be consistent across the range of a tree species (see section below “Standing Genetic Variation in the Context of Range Position”), and resistance may involve trade-offs with other traits such as growth, drought resistance, seed production, tissue palatability, and nutrient dynamics that have implications for ecosystem function (Reid et al., 2016; Lovett, 2018). Additionally, the longevity of trees relative to their pests means that the latter have the potential to evolve more rapidly than their hosts.

The Importance of Maintaining Standing Genetic Variation for Forest Health

An important difference in the forest tree situation from agricultural uses of biotechnology is that a focus on recovering forest species requires incorporating the specific genetic change while retaining the breadth of genetic diversity in forest populations. This diversity permits the species to continue to evolve under changing abiotic and biotic conditions (see “Site Management Practices” in Chapter 3). Provenance studies in many tree species have revealed substantial variation in response to environmental factors; variability that will be critical for potential adaptation of species to environmental changes (e.g., Aitken and Bemmels, 2016; Montwé et al., 2018). Adaptation to local environmental conditions often require different breeding populations for different portions of the species’ geographic range. As a result, to maximize forest health, the genetic changes need to be incorporated into a diverse breeding population rather than into an individual cultivar or variety.

Standing Genetic Variation

Long-lived forest tree species often have wide geographical distribution and exhibit predominantly outcrossing mating systems. As a consequence, much of the genetic variation in populations of forest trees is partitioned within populations and very little among them (Hamrick, 2004) with some exceptions (see Kinloch et al., 2003). Standing genetic variation is the amount of allelic variation at a genetic locus that is segregating within a population (Orr, 2005). This variation, shaped by evolutionary and demographic forces, provides raw material for rapidly adapting to the changing environment as well as to novel habitats during range expansion (Barrett and Schluter, 2008). When an allele confers a functional benefit (e.g., resistance to an insect pest or disease), natural selection may act upon it and drive it to fixation in the population. The genetic locus then no longer constitutes part of the standing genetic variation. Additionally,

mutations arising *de novo* in populations may also provide a secondary source of genetic variation for adaptation through the action of natural selection, but the mutation rate is very low in forest tree species (Savolainen and Pyhäjärvi, 2007). Thus, standing genetic variation is the primary vehicle for evolutionary change and is highly consequential for forest health, the forest's adaptability to environmental change, and the resilience of the forest to insect pests and pathogens.

Standing Genetic Variation in the Context of Range Position

The distribution of a species' standing genetic variation across its range has historically been studied in terms of population position at range center versus range margin vis-à-vis the classical central marginal hypothesis (Eckert et al., 2008). Theoretical predictions of the hypothesis suggest diminished levels of genetic variation at range margins where environmental conditions are usually at the limits of physiological tolerance, in contrast with the abundant center where conditions are conducive to maintenance of optimal levels of genetic variation. While there is some support in literature for this prediction, the debate around this issue is not fully resolved. A synthesis of the evolutionary and demographic dynamics at various parts of a species' distribution range (Hampe and Petit, 2005) may suggest that the warmer rear-edge populations may contain genetic variants preadapted to the environmental conditions that are forecasted for the northern latitudes under climate change. Experimental evidence is limited but is continuing to accumulate for this prediction (e.g., Rice et al., 1993). In particular, understanding the patterns of radiation out of the glacial refugia (i.e., geographic regions where flora and fauna survived during the ice ages and later recolonized postglacial habitats) and how that has shaped the standing genetic variation in response to past climates is important when choosing genetic backgrounds against which to deploy biotechnological solutions to climate or pest mitigation. Assisted migration by humans of forest trees to mitigate the effect of climate change on tree species is being considered. In these cases, such preadapted variants may provide the key to healthy forests in geographically distant but environmentally similar (as a result of climate change) habitats. This knowledge base of population-level adaptive standing genetic variation together with data from ecological factors and climate modeling could provide clues to adaptability of forest tree populations to climate change through either migration or adaptation (Neale and Kramer, 2011).

Range expansion and contraction have been part of the evolutionary history of most tree species. During repeated climatic oscillations, advancing glaciation forced forest tree populations into refugia at both southerly latitudes in North America as well as in the Pacific Northwest (Shafer et al., 2010). Receding glaciers allowed species to expand to higher latitudes out of these refugia. Thus, the standing genetic variation in the refugia is a product of eons of demographic and evolutionary forces and thus likely to contain variants that are preadapted to a variety of environmental conditions. The current distribution of loblolly pine (*Pinus taeda*) is, for example, hypothesized to have radiated from two southern refugia, one in Florida and another in Mexico (Schmidtling, 2003). Similarly the glacial refugia for *Populus* are predicted to have existed in the Rocky Mountain region (Levsen et al., 2012), which constitutes the present-day southern-range edge of balsam poplar (*Populus balsamifera*), a boreal tree with one of the widest distributions in northern North America. Red maple (*Acer rubrum*) has been shown to have taken refuge in the unglaciated Appalachian Mountains, south of the Laurentide ice sheet (Delcourt and Delcourt, 1984). A similar pattern was observed in American beech (*Fagus grandifolia*) (McLachlan et al., 2005), whose refugium was located immediately south of the glaciation, whereas the western redcedar (*Thuja plicata*) is hypothesized to have expanded in the previously glaciated northern region out of a coastal refugium off Washington and south of the glaciation (Barnosky et al., 1987). Thus, historical distributions of tree species have contributed to their standing genetic variation, a factor that needs to be considered when assessing forest health and tree resistance to pests.

Local Adaptation and Its Genetic Basis

A genotype or a population is locally adapted when its fitness is higher under the local environment, but exhibits lower fitness elsewhere (Savolainen et al., 2007). In forest trees, many of these locally adaptive

traits are complex in that their underlying architecture is controlled by multiple genes (Savolainen et al., 2007). Understanding the genetic basis of such complex traits remains a foremost goal in all of biology because of its implications for human health, agriculture, forestry, and ecosystem conservation and management. Given the postglacial phylogeographic history of forest tree species, local adaptation is likely widespread among their populations. Recent studies of many temperate forest tree populations have revealed strong latitudinal adaptation to the environment (e.g., temperature and photoperiod) for quantitative traits such as flowering phenology, growth, cold and drought tolerance, and ecophysiology (Howe et al., 2003; Savolainen et al., 2007; Aitken et al., 2008; Alberto et al., 2013; Olson et al., 2013; Guy, 2014). Landscape genetics/genomics is a relatively new field of research that aims to understand the landscape-level processes leading to local adaptation in widely distributed taxa (Manel et al., 2003; Manel and Holderegger, 2013). This field has leveraged the rapid advances and exponential growth in sequencing technology coupled with theoretical and methodological developments (Sork et al., 2013; Lotterhos and Whitlock, 2015) to facilitate genome scans to understand local adaptation.

Given their substantial diversity and complex phylogeography, the knowledge base of adaptive standing variation and local adaptation in forest trees is limited, but the availability of novel analytical tools (ecological, climatic, genomic, and computational) is paving the way for a better understanding of their adaptive potential. Considering the multitude of threats facing forests and projected climate change over the next century, some researchers have proposed assisted gene flow between populations to facilitate forest survival in the 21st century and beyond (Aitken and Whitlock, 2013; Dumroese et al., 2015; Aitken and Bemmels, 2016). Any biotechnological approach, when combined with this assisted migration, would need to be fully informed by a thorough understanding of the extent of standing genetic variation and patterns of local adaptation within the species. One species where such studies have been conducted is whitebark pine, whose populations have sustained heavy losses due to a multitude of factors (see section “Case Study Trees” in Chapter 2). Rangewide as well as local-scale population genetic analyses and common garden experiments have revealed adaptation for growth and survival (Warwell, 2015), cold (Bower and Aitken, 2008), drought (Warwell and Shaw, 2017), soil water availability (Lind et al., 2017), and growth rhythm (Warwell and Shaw, 2018) along climatic gradients in whitebark pine. This finding has led to the development of seed transfer (assisted migration) guidelines for restoration purposes (Bower and Aitken, 2008), which have subsequently been employed to test the potential of the species to grow successfully beyond its northern range-margin (McLane and Aitken, 2012). The results from that research suggests that assisted migration could be a promising first step in the restoration of threatened species when information on standing variation and local adaptation is coupled with climate and species distribution modeling. A series of common garden field trials of whitebark pine have recently been established to help more fully understand the adaptive genetic variation in whitebark pine and provide field validation of resistance to white pine blister rust (Cartwright et al., 2016; Cartwright, 2018; USDA–FS, 2018). Monitoring these trials over the next several decades will improve understanding of how to best restore whitebark pine forests in the future.

Disruption of Local Adaptation Under Climate Change

When considering assisted migration as a potential restorative tool, it would be important to keep in mind that impending climate change may disrupt existing *gene* × *environment* associations (i.e., local adaptation), resulting in maladaptation. For widely distributed tree taxa, some parts of the range may be more vulnerable to such disruption than others. For example, strong adaptation to climate and photoperiod in phenological traits is known to occur in the case of *Populus balsamifera* (Soolanayakahally et al., 2009; Keller et al., 2012). Fitzpatrick and Keller (2015) demonstrate through modeling of various future climate scenarios where along the spatial landscape local adaptation will be disrupted. Using variation in *GIGANTEA 5*, a circadian-clock gene with strong local adaptation to temperature, they show that northernmost populations of *P. balsamifera* will likely experience the largest “genetic offset” from the adaptive optima. Genetic offset due to future patterns of changing rainfall have also been predicted in populations of Hawaiian koa trees (*Acacia koa*) and may inform reforestation and seed transfer guidelines (Gugger et al., 2018).

Thus, a biotechnological approach would need to account for the standing genetic variation and the extent of local adaptation and avoid swamping local adaptation or introducing maladapted genotypes while also supporting natural gene flow. It would also be prudent to identify populations which may likely experience genetic offset due to the disruption of local adaptation through climate change.

ECONOMIC CONSIDERATIONS

The committee identified the economic considerations of deploying a biotech tree resistant to insect pests or pathogens through the resulting impacts on ecosystem services. First, the significant economic value of forests to humans is one important motivation for intervening to maintain or restore forest health through the introduction of a biotech tree. Second, the incentive for the public and private sectors to invest in the development of such a biotech tree is conditioned by the types of benefits its introduction is expected to provide, largely dependent on whether the anticipated gains in goods and services are traded and priced in markets. Third, the eventual introduction of the biotech tree will raise issues around consumer acceptance of the goods and services obtained, preferences that may be reflected in third-party certification schemes.

Economic Value of Forests

The natural resources of the U.S. forests support both private and public uses. In the United States, one-third of all land area is forested, more than 300 million hectares out of 980 million total (Oswalt et al., 2018). Timberland accounts for two-thirds of forestland, with about 13 percent of that land being planted and the rest in forest of natural origin. With regard to ownership of forestland, just over 40 percent nationally belongs to federal, state, tribal, local, and municipal governments, with the other 60 percent in private hands. Changes in nondisclosure laws pertaining to data-reporting mean that it is no longer possible to distinguish corporate from noncorporate private ownership. However, to the extent that corporate ownership is associated with tree plantations, the lower bound of corporate control could be around 9 percent of forestland, which would be about 13 percent of timberland. These percentages vary regionally. For example, public entities own three-quarters of timberland in the intermountain West, but only about one-fifth in the Southeast. Overall, U.S. forests vary with respect to ownership and geographic distribution (see Oswalt et al., 2018, for more detail).

There are three main components of the private forest industry (U.S. Census Bureau, 2017):

1. Forestry and logging (growing and harvesting on a long production cycle, more than 10 years);
2. Wood product manufacturing (lumber, plywood, veneer, containers, flooring, etc.); and
3. Paper manufacturing (pulp, paper, paper products).

As components of Gross Domestic Product (GDP), altogether these sectors accounted for about 0.5 percent in 2017 (BEA, 2018). Wood-products and paper-sector value added was about 5 percent of manufacturing GDP, which itself accounts for 12 percent of GDP. Employment in all three sectors has been just under 1 million people in recent years, out of a total workforce of 125 million (BLS, 2018).

The value added by activities on public lands is harder to quantify because of the nonmarket, non-commercial nature of ecosystem services. National income accounts do not recognize the contributions of forests in providing fish and wildlife habitat protection, watershed protection, carbon sequestration, and many other ecosystem services (FAO, 1998). Integrated economic and environmental accounting would provide a more complete picture of U.S. wealth and income from forests, but this approach has not been pursued by statistical agencies at the national level in recent years. The U.S. Bureau of Economic and Business Affairs produces satellite accounts for outdoor recreation (about 2 percent of GDP in 2016) and for travel and tourism (about 3 percent in 2016). Forests, of course, support only some part of these activities.

Outside the official national accounts, researchers have employed various techniques to value forests in monetary terms. Based on the concept of ecosystem services, one estimate pegged the value of boreal

and temperate forests at \$3,137 per hectare per year (2007 U.S. dollars) (Costanza et al., 2014). Of the global total, the United States is about 8 percent or 310,095,000 hectares (FAO, 2016). Based on that estimate of area and per-unit value, the total value of U.S. forest ecosystems would be roughly \$975 billion (for comparison, U.S. GDP in 2007 was about \$14 trillion). With a narrower focus, the recreational value of the U.S. National Forest System has been estimated at about \$14 billion averaged over the period of fiscal years 2011 to 2015 (Rosenberger et al., 2017). Filtration of airborne particulates by U.S. forests in 2010 had an estimated value in human health benefits of \$6.8 billion (Nowak et al., 2014). These estimates are made with varying assumptions and can only be considered very approximate; valuation of ecosystem services is a fraught task, and some important services, particularly associated with nonuse value, are not easily expressed in monetary terms at all. However, such estimates do suggest robust value for the nation's forests, even without taking forests' noninstrumental values into account. In some cases, it may be possible to avoid diminution of that value due to damage by insects and diseases, and possibly even reverse losses, by the introduction of biotech trees. Still, assessment of the value to be restored or protected by the introduction of any one tree can only be made with reference to the particular uses and characteristics of the forest ecosystem in question.

Incentives to Invest in the Development of a Biotech Tree

When a forest ecosystem is threatened, the motivation to restore it to health is conditioned by concerns about the ecosystem services that are adversely affected or diminished when a tree species is lost or declining. The introduction of a biotech tree may thus be expected to affect the services provided by the forest ecosystem of which it is a part. Changes in these services can imply changes in the human uses and benefits derived from these services. To be able to assess these changes in terms of their economic significance, it is useful to review the classification of ecosystem services in a use/nonuse framework of total economic value (Pearce et al., 2006). Use value arises from the actual, planned, or possible use of a service. For example:

- An extractive use might be the harvest of timber for use as a biofuel.
- An in-situ use might be hiking or bird watching or contemplating the aesthetic beauty.
- Option value might arise because of a desire to preserve the possibility of future use of the forest and its services.

Nonuse value stems from the benefit that arises even if there is no actual or planned use of the service.

- Existence value might derive from the knowledge that old-growth forests exist, even if no human visit were ever to occur (see section “The Value of a Healthy Forest” in Chapter 2 for further discussion).
- Bequest value would reflect a concern for the ability of succeeding generations to use the services, as with the 1892 creation of “forever wild” Adirondack Park.

Uses and nonuses affected by the introduction of a biotech tree may be embodied in market goods (such as the extractive use of timber for biofuel) or may be considered as public goods or benefits not traded or priced in markets (such as the existence of a stand of old-growth trees). These distinctions matter when evaluating incentives to develop biotech trees.

Trees, once planted and maturing, can provide both use and nonuse values as reflected in either public or private benefits. Public benefits are those that cannot be exclusively captured by an individual or a firm but are shared across many people and communities. Examples include clean air and water, flood control, support for biodiversity, and scenic landscapes (USDA-FS, 2007). In contrast, private benefits flow from extractive uses, such as logging, products that can be exclusively held and sold in markets by firms and individuals. As would be expected, then, investment in the development of trees to provide mainly public

goods—such as resistance to insect pests and pathogens—is usually pursued by governments and by non-profit entities. Commercial forestry is the purview of firms with a profit motive.

The significance of the mix of public and private benefits of a biotech tree to the incentives to develop it can be illustrated with two examples. One is the freeze-tolerant eucalyptus for private planted forests and the other is the blight-resistant chestnut tree for less managed public and private forests.

- The freeze-tolerant eucalyptus is to extend northward toward the range of its use as a plantation tree in the southeastern United States. These nonnative, biotechnological trees are fast-growing and could provide timber and pulpwood, as well as a source of lignocellulose for the production of energy and advanced biofuels (Hinchee et al., 2011). Although these trees can provide public benefits as well (such as effects on air quality), the main incentive for their development is the potential for the sale of their products in markets. Accordingly, the private firm Arborgen has been the developer of the freeze-tolerant tree.
- The blight-resistant chestnut tree similarly can provide benefits in the form of marketable commodities (e.g., wood and chestnuts), but its developers are organized as a university and a nonprofit foundation. The release of the tree into less managed or unmanaged forests may result in its restoration as a key ecosystem species and also in the aesthetic and cultural appreciation it enjoyed when it dominated regions of the northeastern U.S. forests (see section “Case Study Trees” in Chapter 2). These aims have strong public-good aspects.

Private firms have the incentive to introduce a tree that provides appreciable returns to sale of its products in markets, whereas public entities are more likely to value its ability to provide public goods that are unlikely to generate market revenue. It is the case that federal and state governments may earn some revenue from timber sales on public land and may support research to enhance productivity of commercial forestry. In the current context, however, public interest would be in innovations that protect forest health, broadly defined and with many public good aspects.

The potential for a biotech tree to yield market and/or public goods and services depends on the particulars of the changes in uses and nonuses that occur when it is introduced into a forest ecosystem. Depending on the mix and the size of the market or public benefits to be had, the private or the public sector may take the lead in development. Moreover, the incentive to apply biotechnology in trees is strongly conditioned by the relatively long time between a tree’s planting and its reaching maturity. Compared to agricultural field crops, which are typically harvested annually, tree crops’ life cycle covers multiple growing seasons, measured in years. As a result, the benefits of tree development and planting may not accrue until far into the future, whereas much of the cost of planting may occur right away. In such circumstances, the economics depend on the time value of money, that is, the opportunity cost of using funds to plant trees and wait for returns versus investing the money in an activity that yields returns much sooner.² This element of delay between planting and maturity has significance for decision making in both the public and private sectors.

The aims of introduction of a biotech tree may be more oriented to generation of revenue from market or more aligned with outcomes associated with public goods. Whether it is a private or a public interest, resources are required to support the research and development (R&D) necessary to bring forth a biotech tree. The potential for forest biotechnology depends on public and private investment in its R&D. The 2002 National Research Council report *National Capacity in Forestry Research* found that, despite apparently large returns to forestry R&D, there were significant gaps in basic biological knowledge and deficiencies in understanding of forest health, systems, and management and wood science (NRC, 2002). More recently, a blue ribbon panel report from the U.S. Endowment for Forestry and Communities asserted that innovation in the sector has slowed over the past several decades (Jolley et al., 2017). This panel estimated U.S. forestry R&D at \$700 million annually, with the federal government accounting for \$500 million, state governments

²See Sedjo (2006) and, for a detailed exposition of the use of the discount rate in decision making (especially for regulatory purposes), see EPA (2014).

for \$150 million to \$175 million, and nongovernment entities for \$10 million to \$15 million. The panel did not address biotechnology specifically, but it did note opportunities to enhance both traditional forest products (e.g., engineered solid wood products and midrise buildings) and nontraditional forest products (e.g., carbon sequestration, renewable energy production).

The willingness of private firms to invest in research is a function of costs and expected returns. The panel from the U.S. Endowment for Forestry and Communities reported that corporate research in the forest sector, at 0.5 percent of annual revenues, is far below that of other sectors, such as biomedical science (including molecular biology) and health care (almost 12 percent of revenues) and automobiles (3.5 percent). The portion devoted to biotechnology was not estimated. Despite this relatively low level of investment, there are incentives to invest in insect pest and pathogen control and in product innovation. For example, losses to timber producers due to tree damage by the southern pine beetle (*Dendroctonus frontalis*) have been estimated at \$43 million annually and \$1.2 billion over about a 30-year period (Pye et al., 2011). Even if conventional tree breeding and biotech tree development had comparable costs for R&D, use of biotechnology comes with the added expense associated with regulatory approval.³ Compliance costs associated with the development of herbicide-resistant maize have been estimated at \$6–\$14.5 million and for insect-resistant maize at \$7–\$15 million (Kalaitzandonakes et al., 2007). If forest biotechnology compliance costs were comparable, two or three passes through the regulatory system would represent about 5 percent of all forestry R&D spending. Whether those costs can be justified will depend, of course, on the particulars of the tree under consideration, but they are a unique factor in assessing investment in biotechnology R&D prospects. Given the relatively long time to benefits accruing with tree maturity, increasing the upfront costs of development may adversely affect the incentive to invest in forest trees.

Public investment in forestry research may be intended to support private-sector economic development, or be aimed at enhancing the societal benefits forests that provide, or both. The federal government has been responsible for the largest investment in tree breeding in concert with states (Jolley et al., 2017). Nonprofit entities, such as foundations, may also invest, as has been the case with the American chestnut. Underinvestment in public goods is a market failure that can be addressed by public intervention. Motivating and justifying spending on forest R&D depends on the identification of the scope and magnitude of the public benefits arising from improvements in forest health and in ecosystem services. (This proposition is true for any kind of effort, whether it be targeted to the use of biotechnology or not.) Consequently, multidisciplinary efforts to characterize these benefits play a role in creating arguments for public expenditures (Boyd et al., 2016). It is also the case that these benefit estimates have value in the context of regulatory decision making when weighed against the costs and risks of introducing a biotech tree. Although the challenges to assessing nonmarket values of these public goods are considerable, there are nonetheless methods (such as contingent valuation) currently being employed in the regulatory process (EPA, 2014).

Proposals for forestry R&D compete with other demands on public resources. Given that the benefits of tree development may occur far into the future, it can be challenging to acquire public funding given competition from activities with a more immediate payoff. Moreover, because the beneficiaries of the investment may be numerous and geographically dispersed, advocacy by a distinct constituency may not be present. Public concern about the use of biotechnology in a forest setting (discussed in the section below, “Current Research on Public Views”) may also affect the willingness of public officials to commit resources. In fact, public spending on forestry R&D has not increased in recent years. There is recognition of this situation in calls for public–private partnerships to pursue projects that had in the past been funded by federal and state sources (Jolley et al., 2017).

Whether R&D is done in the public or private sector, the assignment of intellectual property rights associated with an innovation can affect its adoption and use. A private firm may seek to recoup the upfront costs of development and regulatory approval by patenting that protects its revenue stream and possibly enhances it through licensing. However, to the extent that the public sector would wish to enable the spread

³Costs associated with the regulatory approval process in the United States for biotech plants is discussed in detail in Chapter 6 of *Genetically Engineered Crops: Experiences and Prospects* (NASEM, 2016b).

of an insect- or disease-resistant biotech tree, then patenting would not seem to be consistent with widespread adoption. Graff and Zilberman (2016) discuss this dynamic of the public interest in “orphan” crops not attractive for commercial purposes and suggest that the presence of significant social benefits motivates development by the public sector. In addition, ethical objections to patenting may arise, for example, over the propriety of patenting living organisms.

The emergence of CRISPR and other genome-editing techniques raises questions about their use by the public sector in development of a resistant biotech tree. At the time the committee was writing its report, there were a number of competing patents and patent applications (Cohen, 2018). However, one key patent holder, the Broad Institute, will not require licensing of its CRISPR innovations for academic and nonprofit use. Specifically, it states, “Nonprofit institutions and government agencies do not need to receive a written license from Broad to conduct internal research, including sponsored research, to the extent that such research does not include the production or manufacture for sale or offer for sale or performance of commercial services for a fee.”⁴ So it would seem that CRISPR-enabled resistance in a biotech tree would preclude the tree’s commercial sale, which might well be consistent with the public interest in protecting forest health.

Consumer Preferences

Another consideration specific to the development of biotech trees is the nature of the markets into which private goods such as timber and pulpwood are sold. Motivated by concerns about the sustainability of the use of forests globally, consumers have sought assurance that the tree products they buy are produced with practices compatible with that aim. Usually, it is not obvious from inspection of the product how the tree was grown. Consequently, third-party organizations now provide certification to consumers that the trees used for making the product are cultivated and harvested in accordance with specified methods that are supposed to promote sustainable use of forest resources.⁵ At the time the committee was writing its report, some forest certification programs applied in the United States prohibited the use of biotechnology. For example, based on its embrace of the precautionary principle,⁶ the Sustainable Forestry Initiative (SFI) has restrictions on the use of biotech trees until the end of 2022. However, SFI policy statements recognize the evolving nature of the underlying science and the potential benefits of biotech trees and state that it will “proactively review and update ... this policy as necessary” (SFI, 2015). Depending on the extent of adoption of such certification in the market, the introduction of biotech trees may be discouraged. At the time the committee wrote its report, it was difficult to judge whether such prohibitions against the use of biotechnology will endure as knowledge about the science and the specific properties and expected impacts of biotech trees become better known.

SOCIAL AND ETHICAL CONSIDERATIONS

Alongside ecological and economic considerations, any proposed use of biotech trees involves taking a variety of social and ethical issues into account. Social science studies provide some information about public views, and how the use of biotechnology in forests is likely to be understood by the public in relation to risk and to alternative tools for addressing threatening forest diseases. Other concerns relate to the ways people value forests, including forests’ wildness and naturalness, how people interpret the use of biotechnology as a conservation tool, and how the use of biotechnology in forests is likely to affect social justice.

⁴Broad Institute. Information about licensing CRISPR genome editing systems. Available at <https://www.broadinstitute.org/partnerships/office-strategic-alliances-and-partnering/information-about-licensing-crispr-genome-edition>. Accessed November 21, 2018.

⁵FAO. Sustainable Forest Management (SFM) Toolbox. Available at <http://www.fao.org/sustainable-forest-management/toolbox/en>. Accessed November 21, 2018.

⁶According to the European Parliament, “The precautionary principle enables decisionmakers to adopt precautionary measures when scientific evidence about an environmental or human health hazard is uncertain and the stakes are high” (www.europarl.europa.eu).

Current Research on Public Views

A number of studies have examined societal views on forest health threats such as insect pests and pathogens (e.g., Flint, 2006; McFarlane and Watson, 2008; Chang et al., 2009; Flint et al., 2009; Müller and Job, 2009; Mackenzie and Larson, 2010; Kooistra and Hall, 2014; Poudyal et al., 2016). However, in comparison to the many studies examining societal views about the use of biotechnology in agriculture and food (e.g., Finucane and Holup, 2005; Costa-Font et al., 2008; Frewer et al., 2013; Lucht, 2015), there have been substantially fewer on views toward using biotechnology in trees to address forest health threats (for a table of these studies, see Appendix D). Most of these studies have been conducted in Europe and Canada, with only a few in the United States. The primary focus of most of these studies has been on biotechnology use aimed at increasing timber in forest plantations (e.g., faster tree growth, better wood structure) or responding to climate change, with only a few recent studies on using biotechnology for restoring tree species or reducing insect pests and pathogens in forests.

Understanding societal responses is important for multiple reasons. First, democratic governance of emerging technologies in forests and elsewhere requires attention to societal views and concerns. Second, given the variety of approaches available when confronting a threat to forest health, scientists and land managers may wish to align their actions with the preferences and values of citizens and other groups to build confidence and trust, avoid controversy, or both. Third, since the advent of the environmental movement in the United States in the 1960s, a broad spectrum of people demand and expect involvement in natural resource management issues with some even seeking co-management with agencies. Complicating these objectives, however, is the existence of multiple “publics” with interests in trees and forests (e.g., citizens or residents, government agencies, companies such as growers and processors, direct and indirect consumers of forest products, and environmental groups; Davison et al., 1997; Sedjo, 2010). Discontented groups can resort to administrative appeals, court cases, protests and demonstrations, ballot initiatives, and direct action if they perceive that their concerns are not being addressed. These societal responses, which can be influenced by the attitudes, norms, perceived risks and benefits, knowledge, trust, and values among citizens and other publics (e.g., agencies, companies), may affect the adoption and management of biotechnology tools in trees and forests (Sedjo, 2006; Gupta et al., 2012; Strauss et al., 2017).

Attitudes and Norms

Although the potential use of biotechnology in trees and forests has raised concerns among some people, as illustrated by monikers and catchphrases such as “Frankenstein Forests,” “Frankentrees,” “Designer Trees,” “Silent Forests,” and “Terminator Genes” (Hall, 2007; Gamborg and Sandøe, 2010; Lombardo, 2014; Porth and El Kassaby, 2014), a majority of the relatively limited number of published studies have shown somewhat positive attitudes and normative acceptance among the majority of citizens and several other publics (e.g., agencies, companies). *Attitudes* involve evaluating something, such as biotechnology, with some degree of favor or disfavor (i.e., like, dislike; good, bad), whereas *norms* are standards that individuals use for evaluating their acceptance of something and whether they think it should be allowed (Eagly and Chaiken, 1993; Vaske and Whittaker, 2004; Fishbein and Ajzen, 2010).

Most studies have reported that although people are most supportive of natural regeneration, selective breeding and planting of native tree species, and site management practices such as thinning and felling to address forest health threats, the majority also support some biotechnological approaches, and many of these methods are viewed as more acceptable than doing nothing in the face of severe threats to forests (Hajjar et al., 2014; Hajjar and Kozak, 2015; Nonić et al., 2015; Fuller et al., 2016; Needham et al., 2016; Jepson and Arakelyan, 2017a,b). Both Hajjar et al. (2014) and Hajjar and Kozak (2015), for example, reported that approximately 85–90 percent of their respondents living in Western Canada accepted the breeding of native species to address forest health threats from climate change, and approximately 50 percent also accepted the planting of trees with traits introduced via biotechnology, but only 35 percent accepted no interventions. A more recent study also in Western Canada, however, found that only 25 percent of residents were supportive of using biotechnology in reforestation efforts in response to climate change

(Peterson St-Laurent et al., 2018). Needham et al. (2016) found that U.S. residents considered native tree breeding and other conventional forms of forest management to be most acceptable for addressing chestnut blight in American chestnut trees (68–88 percent), but a majority also supported using various types of biotechnologies for mitigating this issue (53–64 percent). Nonić et al. (2015) found that 56–59 percent of students in universities in Serbia agreed with using biotechnology in trees, and Fuller et al. (2016) reported that 66 percent of UK residents accepted biological control methods (including biotechnology approaches) for managing tree pests and diseases. Adding additional nuance, Jepson and Arakelyan (2017a) found that cisgenic approaches (i.e., genetic modification with genes largely from the same species) were in the top three preferred options (for 54 percent of residents surveyed) among eight courses of action for addressing ash dieback in the United Kingdom, but transgenic methods (i.e., genes from unrelated species) were the least or second-least preferred choice for 85 percent of these residents, suggesting that there is sensitivity to differences among various biotechnological solutions.

Many studies have also reported that biotechnological tools tend to be either just as acceptable or even more acceptable than hybridization with nonnative species (a nonbiotechnological tool). Needham et al. (2016), for example, reported that changing genes in American chestnut trees (57–58 percent of U.S. residents supported this approach in general), such as adding genes from bread wheat (the *OxO* gene; 54–55 percent supported this approach in particular), was more acceptable for addressing chestnut blight than breeding with nonnative Asian chestnut species (43–46 percent supported). Jepson and Arakelyan (2017b) found that only 17–18 percent of their respondents in the United Kingdom preferred breeding and planting nonnative ash to mitigate ash dieback, whereas 27 percent preferred “using genetic modification techniques, including cisgenics and transgenics” (unlike Jepson and Arakelyan, 2017a, cisgenic and transgenic approaches were combined in this later study by the same authors). Both Hajjar et al. (2014) and Hajjar and Kozak (2015) found similar levels of acceptance (approximately 50–60 percent) among Western Canadians for breeding and planting different tree species and planting species altered using a biotechnology approach for addressing threats to forest health from climate change. A more recent study in Western Canada found that 26 percent of residents supported reforestation with nonnative species and, similarly, 25 percent supported using trees containing genetic material altered through biotechnology (Peterson St-Laurent et al., 2018).

Surveys have found that the use of biotechnology in trees and forests is slightly less acceptable than the use of biotechnology in some other industries such as medicine, but more acceptable than using biotechnology in agriculture and food (Connor and Siegrist, 2010). Studies have also shown that people tend to be more supportive of using biotechnology to address immediately pressing and tangible forest health threats, such as insect pests and pathogens, compared to other issues such as climate change or improving tree growth and productivity for increased timber harvesting (Nonić et al., 2015; Fuller et al., 2016; Needham et al., 2016). In a study of university students in Serbia, Nonić et al. (2015) found that, on average, enhancing resistance to diseases was the most acceptable use of biotechnology in trees. Similarly, Needham et al. (2016) reported that biotechnological approaches were slightly more acceptable among American residents for addressing chestnut blight (53–64 percent) than for mitigating effects of climate change (45–58 percent) or for increasing forest growth and productivity (43–55 percent). Despite these findings, the use of biotechnology is much more acceptable in plantation forests than in noncommercial forests. Jepson and Arakelyan (2017a), for example, found that only 38 percent of UK residents approved of planting cisgenic or transgenic ash trees in woodlands, but 60 percent supported planting these trees in forest plantations. Likewise, Kazana et al. (2015, 2016) reported that the majority (56–93 percent) of university students in 15 European and non-European (e.g., Argentina, Israel) countries approved of growing transgenic trees in plantations.

Attitudes and norms toward the use of biotechnology in trees and forests also vary among citizens and other interest groups (e.g., agencies, nongovernmental organizations [NGOs], scientists; Friedman and Foster, 1997; Strauss et al., 2009; Needham et al., 2016; Nilausen et al., 2016). Nilausen et al. (2016), for example, found that government (78 percent support) and industry (100 percent) representatives had highly positive attitudes toward using tools related to biotechnology in trees and supported their continued research and use in Canada, whereas environmental NGOs (50 percent) and indigenous groups (17 percent) had far

less positive attitudes. Needham et al. (2016) reported that, compared to American citizens (53–64 percent support), other groups involved in forest issues (e.g., scientists, agencies, companies) had more positive attitudes (81 percent) toward using biotechnology to address chestnut blight. Conversely, Hajjar et al. (2014) found that although approximately 50 percent of Western Canadian residents supported planting genetically engineered trees to help forests respond to climate change, only 30 percent of community leaders (e.g., elected officials such as mayors, council members, and town managers) supported this approach. Friedman and Foster (1997) reported that government managers and scientists in the United States were concerned about potential impacts of using biotechnology in trees and forests (e.g., possibility of reducing genetic diversity). However, in a study of government, university, and private-sector scientists in both Canada and the United States, Strauss et al. (2009) found that more than 70 percent believed regulatory requirements are significant impediments to research on forest biotechnology, and that the use of biotechnology in trees should be encouraged.

Perceived Risks and Benefits

These attitudes and norms associated with the use of biotechnology in trees and forests are influenced by cognitive factors such as *risk perceptions* (Connor and Siegrist, 2010), which are subjective and negative evaluations of threats posed by potential hazards (Slovic, 2000, 2010). Objective risk is defined as the calculated probability and consequences of potential hazards, whereas perceived risks are subjective judgments that draw upon intuitions and other heuristic processes (Slovic, 2000, 2010). For example, people often express more concerns about new, unknown, and unnatural hazards that are not well understood or are outside of their control (Slovic, 2000, 2010; Sjöberg, 2004; Finucane and Holup, 2005), and this means that these risks are often perceived as more significant than other hazards that are more common and well known, but have higher objective risk.

Given their novelty, biotechnological approaches for modifying forest trees are expected to be perceived as riskier than familiar methods such as selective breeding (Strauss et al., 2017). As mentioned above, research examining societal responses toward methods for mitigating forest health threats showed that biotechnological approaches were often perceived as less acceptable than more familiar approaches such as tree breeding, planting, thinning, and felling (Hajjar et al., 2014; Hajjar and Kozak, 2015; Needham et al., 2016; Jepson and Arakelyan, 2017a,b; Peterson St-Laurent et al., 2018). Yet, such responses are not entirely consistent, because breeding with related species (e.g., American chestnut with nonnative Asian chestnut, native ash in the United Kingdom with nonnative ash) was considered by citizens to be riskier compared to some cisgenic (e.g., altering genes in native ash in the United Kingdom; Jepson and Arakelyan, 2017a,b) and transgenic approaches (e.g., inserting genes from unrelated species such as from bread wheat [i.e., the *OxO* gene] into the American chestnut; Needham et al., 2016), suggesting that perceptions of naturalness or familiarity may elicit different concerns in some cases. For example, Asian chestnut species are more closely related to the American chestnut than wheat is, but are not as familiar to Americans as wheat (i.e., as a source of bread; Strauss et al., 2017). Although speculative, it may also be that concerns about naturalness and purity of species are driving some preferences, as the transgenic tree maintains a higher percentage of American chestnut DNA than a backcrossed tree with DNA from both the American and Asian chestnut species (Nelson et al., 2014; Powell, 2014). In fact, recent research in Western Canada showed that perceived transgressions of naturalness drive resident perceptions of risk and levels of support more than the biotechnological intervention itself (Peterson St-Laurent et al., 2018).

Sjöberg (2004) identified interfering with nature and severity of consequences as two other important dimensions of risk perceptions related to biotechnology in general (not necessarily related to forestry or in any specific location). The same societal concerns about risks associated with humans manipulating, tampering, and interfering with nature have been found in studies of biotechnology in trees and forests in Western Canada (Hajjar and Kozak, 2015) and the United Kingdom (Jepson and Arakelyan, 2017b). People have also perceived that severe changes in ecosystem components and functions are among the largest risks of forest biotechnology. For example, respondents in several studies in Canada and Europe were concerned

that altering genes or adding transgenes in plantation trees could change genes or reduce the genetic diversity of wild or native trees (through gene flow), causing long-term impacts on biodiversity that are currently unknown (Kazana et al., 2015, 2016; Nonić et al., 2015; Tsourgiannis et al., 2015, 2016; Nilausen et al., 2016) and potentially increasing legal and liability concerns (Strauss et al., 2009). Additional concerns included vulnerability to other tree diseases and impacts from more pesticide inputs (i.e., from using disease-, herbicide-, and insect-resistant traits; Kazana et al., 2015, 2016; Nonić et al., 2015). Taken together, these findings are consistent with those of Lorentz and Minogue (2015), who examined perceived risks of eucalyptus plantations in the southeastern United States and found that invasion potential and associated negative ecological impacts on nonplantation forests were primary concerns. Similarly, Friedman and Foster (1997) surveyed U.S. forest agency employees⁷ and found that loss of adaptation, reduced genetic diversity, and changes in ecosystem components were the largest perceived risks from the use of biotechnology in trees and forests.

In addition to these risks, attitudes toward using biotechnology in trees and forests may also be related to the extent that people view these approaches as beneficial. Research mostly in Canada and Europe has found that respondents in several studies *perceived benefits* of forest biotechnology, including:

1. Increased tree growth and productivity (Kazana et al., 2015, 2016; Nonić et al., 2015);
2. Economic and community benefits such as greater employment and income, more economic diversification and competition, and reduced production costs and losses (Neumann et al., 2007; Tsourgiannis et al., 2013, 2015, 2016; Hajjar et al., 2014; Hajjar and Kozak, 2015);
3. Greater consumer choice and purchasing options (Tsourgiannis et al., 2013, 2015, 2016);
4. Restoration of contaminated soils (Kazana et al., 2015, 2016);
5. Reduced pressure on harvesting trees from forests if biotechnology is constrained to plantations focused on increasing growth (Nilausen et al., 2016); and
6. Reductions in insecticide, pesticide, and herbicide inputs (Kazana et al., 2015, 2016).

These benefits, however, may differ depending on the type and scale of production (e.g., plantation owners or smaller community forests) as well as the intent of biotechnology use (e.g., to increase timber, protect or restore forests, reduce insects and diseases; Strauss et al., 2017).

Knowledge, Trust, Values, and Communication

Knowledge can also influence attitudes toward biotechnology (Connor and Siegrist, 2010). Some studies in Europe and the United States have shown that the majority of citizens and other publics (e.g., agencies, companies) who have been surveyed are aware of particular forest health threats and have heard about the potential for using biotechnology in trees and forests (Kazana et al., 2015, 2016; Nonić et al., 2015; Needham et al., 2016). Both Kazana et al. (2015, 2016) and Nonić et al. (2015), for example, found that 60–70 percent of their respondents in mostly European countries knew what a transgenic tree was and were aware of the meaning of transgenic trees. However, given the complexity and novelty of biotechnology in trees and forests, many people lack detailed knowledge about specific aspects of this topic (Strauss et al., 2017). Kazana et al. (2015, 2016), for example, found that despite high general awareness about this issue, fewer than half of their respondents in 15 European and a few non-European countries (Argentina, Australia, Israel) could specify benefits or risks and knew whether these trees could be deployed in plantation forestry (e.g., grown commercially, sold on the market). This finding led these authors to believe there was “a serious perceived lack of knowledge about potential benefits and risks of the cultivation of transgenic forest trees” (Kazana et al., 2015:344). Although this does not invalidate the findings of other social science research that can be valuable even when knowledge about specific aspects of a topic is relatively low, it

⁷Friedman and Foster (1997) surveyed employees of the U.S. Forest Service, the Fish and Wildlife Service, and the Bureau of Land Management as well as those at state and local agencies.

serves as a reminder that as various publics learn more about biotechnology in trees and increase their familiarity with this topic, their attitudes, norms, and perceptions of risks and benefits may change. In other words, these societal responses are highly dynamic, contextual, and varied in their intensity.

Respondents in a few mostly European studies believed that labeling and other forms of marketing and promotion could serve as one way of increasing awareness about forest biotechnology (Tsourgiannis et al., 2013, 2015, 2016; Kazana et al., 2015, 2016; Nonić et al., 2015). These studies showed that the majority of their respondents believed that labels should be required on any forest products involving the use of biotechnology, such as final products that originated from cisgenic or transgenic trees. Other European studies have discussed additional methods for increasing information about threats to forests (e.g., insect pests, pathogens, climate change) and increasing knowledge about potential biotechnological interventions for addressing these threats, including news coverage and social media attention (Tsourgiannis et al., 2013, 2015, 2016; Kazana et al., 2015, 2016; Nonić et al., 2015; Jepson and Arakelyan, 2017b). However, a couple of studies have shown that attitudes toward the use of biotechnology in trees and forests are extremely sensitive to informational messages and vulnerable to persuasion campaigns. For example, in an experiment involving samples of adults in the eastern United States and also students in Canadian and U.S. universities, Needham et al. (2016) found that acceptance of biotechnological interventions in trees and forests dropped dramatically (from 75–83 percent down to 40–44 percent) as soon as messages included any negative arguments (e.g., pejorative language) about this topic. Similarly, Hajjar et al. (2014) reported that acceptance changed for many of their Western Canadian respondents after being told that each potential intervention (including planting cisgenic or transgenic trees) would create either positive benefits or negative risks and other outcomes.

Given the lack of detailed knowledge about specific aspects of this topic and the potential malleability and instability of attitudes in response to informational or persuasive messages, trust in knowledgeable experts (e.g., forest agencies, scientists) is an important consideration for understanding perceptions and other responses (Brossard and Nisbet, 2006). *Social trust* is the willingness to rely on those responsible for making decisions or taking actions affecting public well-being (Connor and Siegrist, 2010). People may rely on trusted sources to assess complex or unknown issues. A number of studies in Europe and North America have shown that greater trust in forest managers (i.e., agencies) and scientists is associated with lower perceived risks, higher perceived benefits, more positive attitudes, and greater normative acceptance regarding the use of biotechnology in trees and forests (Neumann et al., 2007; Connor and Siegrist, 2010; Hajjar and Kozak, 2015; Needham et al., 2016; Jepson and Arakelyan, 2017a; Peterson St-Laurent et al., 2018). These trusted sources can use informational campaigns to increase knowledge that people can use for informing their support or opposition toward forest biotechnology in various contexts (e.g., private vs. public land, plantations versus noncommercial forests; Strauss et al., 2017).

However, people may trust forest managers and scientists but may not always listen to them when the information provided conflicts with their own worldviews, beliefs, or values (Kahan et al., 2011; NRC, 2015). *Values* are abstract, enduring, and concerned with desirable end-states (e.g., safety, success) and modes of conduct (e.g., honesty, politeness). Values are basic modes of thinking that are shaped early in life by family or peers, are few in number and relatively stable, change slowly, and transcend situations and objects (Rokeach, 1973; Manfreda et al., 2004). There has been little research examining any potential direct relationships between these general values and more specific attitudes toward biotechnology in trees and forests. However, research has shown that a related, but different, concept called value orientations can be associated with these attitudes (Hajjar and Kozak, 2015; Needham et al., 2016; Peterson St-Laurent et al., 2018).

Value orientations reflect an expression of more general values and are revealed through the direction and strength of basic beliefs that an individual holds regarding more specific situations or issues (Manfreda et al., 2004). To measure value orientations toward forests, for example, Vaske and Donnelly (1999) asked individuals in the United States how strongly they agreed or disagreed with belief statements such as “the primary value of forests is to generate money and economic self-reliance for communities” and “forests have as much right to exist as people.” Patterns among these types of beliefs can be combined into value orientation continuums such as anthropocentric–biocentric, domination–mutualism (i.e., utilitarianism–affiliation or caring), and use–protection (Manfreda et al., 2004; Vaske and Manfreda, 2012). In the context

of biotechnological interventions in trees and forests, Needham et al. (2016) reported that a representative sample of Americans with biocentric or environmental value orientations had slightly more positive attitudes toward using biotechnology to help trees resist chestnut blight and restore American chestnut forests than did those with anthropocentric or utilitarian value orientations. Hajjar and Kozak (2015) found that among a representative sample of Western Canadians, those with mixed or neutral environmental value orientations were slightly more accepting of biotechnology as a solution for addressing impacts of climate change on forests compared to those with more biocentric orientations. A more recent study in Western Canada showed that residents with anthropocentric value orientations were most supportive of using biotechnology in reforestation efforts in response to climate change (Peterson St-Laurent et al., 2018). Although these findings are mixed, they suggest that information campaigns, even from trusted sources, may have limited success in changing the attitudes of some people because these cognitions may be rooted in base values and value orientations that can be difficult to change.

In addition, the discredited *deficit model* suggests that if people are given accurate information from sources that are considered to be objectively trustworthy and reliable (e.g., agencies, scientists), they would be more likely to overcome their limited knowledge and change their opinions to align with these sources (Davison et al., 1997). However, that is not how most people make decisions. In fact, more information about an issue does not always lead to greater knowledge or support, and it may even produce the opposite effect (Scheufele, 2006; NRC, 2015). For example, increased scientific information and communication from trusted sources may actually heighten risk perceptions, leading to more opposition toward the technology (Kellstedt et al., 2008). In addition, many people with limited knowledge about a complex issue (e.g., biotechnology) do not always base their decisions on new knowledge and information from trusted sources (i.e., *cognitive reasoning*). Instead, they often base their decisions on values, emotions, heuristics, schemas, and mental shortcuts, such as information from others who are like them and important to them (i.e., *motivated reasoning*; Brossard and Nisbet, 2006). In the context of biotechnology in forests, for example, critics may rely on intuitions and mental images (Blanke et al., 2015) such as “playing God,” “opposite of natural,” and “forest contamination,” whereas proponents may rely on notions of “technological progress,” “benevolent scientists,” or “wilderness as a managed garden.” This can lead to a *confirmation bias*, which is the tendency for people to seek information that reinforces their own values, supports what they already believe, and rejects disconfirming information even from objectively trustworthy sources (Kunda, 1990; Scheufele, 2006; Brossard and Nisbet, 2006; NRC, 2015).

Social and Ethical Values

As the research on public views outlined above suggests, developing biotechnology for use in trees and forests, especially in noncommercial and less intensively managed public forests, poses not only ecological and economic challenges, but also raises a range of social and ethical considerations. Some of these considerations directly relate to the provisioning of ecosystem services, including the perceived benefits to people and the environment (see Chapter 5 for a discussion of the complexity of ecosystem services), but some social and ethical considerations—especially those relating to intrinsic values of forests and social justice concerns—are not captured in ecosystem services. Although acknowledging that cultural components of ecosystem services provide a fairly broad and inclusive umbrella, this section explores social and ethical considerations as a complement to the ecosystem services framework. These considerations include intrinsic values, including the value of wildness, broad social influences, and social justice concerns.

Biotechnology and Forests’ Intrinsic Value

Because the idea of intrinsic value in nature is important for many conservationists (Justus et al., 2009), one consideration is what impact the use of biotechnology in forests might have on forests’ intrinsic value. The term “intrinsic value” can be used in different ways; the most relevant meaning here is intrinsic value understood as *noninstrumental* value, interpreted as the “value of things as ends in themselves, regardless of whether they are also useful as means to other ends” (Brennan and Lo, 2016). If a forest has

intrinsic value in this sense, it has value in itself, above and beyond any use or service that it may provide human beings (as discussed in Chapter 2). Nonanthropocentric values are not easily captured in terms of traditional definitions and applications of ecosystem services (see, e.g., spiritual values in Box 4-1; see also Chapter 5), although the framework could recognize the benefit that some people experience in recognizing the intrinsic value of a species or ecosystem.

The use of biotechnology in forests has the potential either to reduce or protect their intrinsic value. If biotechnology had the effect of making forests more easily available for human use and benefit, then it could undermine forests' intrinsic value. However, whether it actually has this effect depends both on the purpose of the forests and the purpose of the particular biotechnology being used. Commercial forests are established primarily for consumptive use; they are likely to have significantly less intrinsic (noninstrumental) value than less intensively managed or noncommercial forests (see section "Biotechnology and Forests' Naturalness or Wildness Value" below). Modifying the genome of a foundation or keystone tree species in a less intensively managed forest to increase resistance to an invasive pathogen or insect pest is not a way of *using* the forest for human benefit. Whitebark pine, for instance, though foundational in its ecosystem, has little commercial use; biotechnological changes to increase resistance to invasive blister rust would not make them more easily available for human benefit.

Biotechnology and Forests' Naturalness or Wildness Value

The use of biotechnology, though, may still have implications for intrinsic value, depending on what is actually being intrinsically valued about the forest. One important way in which forests may be valued intrinsically is in terms of their *wildness* or *naturalness*. It should be noted that the meaning, existence, and value of "wild," "wilderness," and "natural" in environments such as forests have been widely contested. A number of scholars have argued that the idea of a valuable "wildness" when located in environments perceived as wilderness or otherwise "set apart" from people is historically and culturally specific, based on a problematic dualism between humans and nature and can lead to devastating impacts on indigenous peoples who occupy such "wild" places (e.g., Denevan, 1992; Cronon, 1995; Callicott and Nelson, 1998; DeLuca and Demo, 2001; Nelson and Callicott, 2008). However, the value of "naturalness" has already played a significant role in debates about biotechnology, and it can be expected that "wildness" will be important in thinking about the use of biotechnology in less managed or unmanaged forests. Where wildness or naturalness are intrinsically valued, there may be significant concerns that biotechnology could reduce this intrinsic value. One widely expressed concern about the use of biotechnology, as some of the research on public opinions discussed above suggests, is that it is considered to be "tampering with nature" or "unnatural" (Sjöberg, 2004; Hajjar and Kozak, 2015; Jepson and Arakelyan, 2017b; Lull and Scheufele, 2017). If biotechnology is seen as extending new, or more intense, human "tampering" into forests previously valued for their naturalness, then biotechnology could be seen as undermining a forests' value in this sense. On the other hand, if intrinsic value is (in part at least) based on the continued natural or wild existence of a particular threatened tree species or population, biological diversity, or the continued health of the entire forest ecosystem, then the use of biotechnology for forest health may be regarded as *protecting* intrinsic value.

When considering biotechnology use in less intensively managed forests (e.g., public, noncommercial), there may be different *kinds* of concerns about unnaturalness. One is a broader concern about the "unnaturalness" of biotechnological processes, the kind of concern that has also been expressed about the use of biotechnology in agricultural crops. Here, "unnaturalness" denotes "whether it could have taken place without human beings" (Siipi, 2015:810). This understanding of "naturalness" may partly explain the findings of Jepson and Arakelyan (2017a), noted above, that in the case of ash dieback in the United Kingdom, cisgenic approaches were preferred over transgenic methods by the residents surveyed. Cisgenesis might be regarded as more "natural" in the sense that it is more likely to occur without human intervention than genetic modification through transgenesis.

BOX 4-1 Forests and Spiritual Values

Spiritual values are frequently included within cultural ecosystem services, most prominently in the Millennium Ecosystem Assessment in 2005 (MEA, 2005). Walking within a forest, for instance, can provide meaningful and satisfying spiritual experiences that may contribute to human self-understanding and sense of place in the world (Rolston, 1998). However, spiritual values related to forests may also include valuing forests *intrinsically* (Moore, 2007). In particular, some spiritual traditions understand entire forests, or individual trees within forests, as being sacred, inspirited, or of moral significance, and therefore as requiring respect or imposing duties, aside from any experiential benefits that the forests might bring (Clark, 2011; Cooper et al., 2016). For instance, many indigenous cultures in North America regard trees as being kin—as brothers and sisters, or relatives, and as part of living communities of which human beings are just another member (Brown, 1985; Booth and Jacobs, 1990; Dockry, 2018). Recent research with Anishnaabe communities in Michigan found that Anishnaabe teachings understand all plants and animals as “persons” who assemble in “nations” and that these beings are kin, part of Anishnaabe extended family (Reo and Ogden, 2018, see also Harwood and Ruuska, 2013, on the personhood of trees among Ojibway communities). It is not clear how the use of biotechnology for forest health would affect, for example, the sacredness of forests or how biotech trees would be regarded in terms of being intrinsically valuable beings or kin. Depending on how biotechnology is understood by these indigenous communities, its use could be interpreted as violating “the right to manifest, practise, develop and teach their spiritual and religious traditions, customs and ceremonies; the right to maintain, protect, and have access in privacy to their religious and cultural sites” (UN, 2006). Further research on the use of biotechnology and spiritual values in forests is therefore needed (see Chapter 7).

However, “unnaturalness” in forests may also refer to wildness understood somewhat differently. Hettinger and Throop (1999:12) defined wildness in a place or thing as “something is wild in a certain respect to the extent that it is *not humanized* in that respect. An entity is humanized in the degree to which it is influenced, altered or controlled by humans.” In the case of forests, wildness might refer to many characteristics such as wild *origins* (humans have not chosen which trees are planted where, but a process of “natural” seed distribution has created the forest); wild *composition* (humans have not decided which species are found where); and wild *processes* (spontaneous evolutionary and ecological processes are continuing without human intervention; humans are not thinning or felling trees, removing dead wood or making other management decisions that control forest processes). The use of biotechnology may be thought to undermine wildness in forests in any or all of these senses by disrupting the perception of wild origins, composition, and processes. Given that biotechnology has the effect of extending human management, influence, and intention, those forests would lose some of their perceived wildness by becoming more entwined with human action.

Any decision to use biotechnology in forests is guided by human preference for a particular future for a forest (e.g., forests should continue to contain specific species), even if that preference is directed at protecting or promoting forest health. To use Hettinger and Throop’s (1999) terms, biotechnology is intended to *influence* and *alter* the forest and could be interpreted as a form of human *control* of a forest ecosystem that previously, in some sense, was “self-directing” or “autonomous.” The use of biotechnology may also affect wildness in the more specific senses mentioned above. For instance, transgenic or genome-edited trees of species chosen by humans are likely to be planted in places selected by humans and for some period at least managed and monitored by humans, which could be understood to reduce wildness in terms of origin, composition, and process value. The use of biotechnology is also a human intervention in the “natural” evolutionary trajectory of the forest. Although the use of biotechnology may promote forest health, it may nonetheless be perceived as diminishing the wildness value of forests. In this sense, debate about forest biotechnology is likely to resemble that of ecological restoration, where concerns have been expressed that the human origin of an ecological restoration makes it less valuable than the original ecosystem, even if the restored system is flourishing and healthy (Elliot, 1982; Katz, 1992).

On the other hand, *threats* to forests that biotechnology may counter are predominantly of human origin (e.g., invasive insect pests and pathogens transported by people and native insect pests and pathogens extending their range because of human influences on climate). Given that these changes are also signs of

human influence, forest wildness may *already* be seen as reduced, if not undermined significantly. Doing nothing to counter such anthropogenic threats may result in the loss of particular populations or entire species, with significant effects on forest ecosystems that at least in some senses (e.g., species composition) also mean a loss of wildness. In addition, other practices that might protect forest health, such as selective breeding, seem to pose rather similar threats to wildness as biotechnology because they also involve the selection of particular genotypes, the decision to plant trees in particular places, continued monitoring of the trees, and so on. So, although the use of biotechnology in forests may diminish their perceived wildness value, alternative options (including, perhaps, no action at all) also reduce wildness, albeit to varying degrees and in different ways.

This can be seen particularly clearly in the case of the whitebark pine's status as "symbols of the primeval forest, the wilderness, and the forces of nature" (Tomback and Achuff, 2010:201). If humans were to intervene in the genome of the whitebark pine, wildness would be reduced in one sense; the genome of all future members of the species would now be influenced by decisions made by humans, which seems to make them less "primeval" and less symbolic of the "forces of nature." On the other hand, whitebark pines are already being threatened by invasive blister rust, introduced by humans planting American white pines that had been grown in Europe and then brought into the United States; without intervention, the whitebark pine may be extirpated in many places, or driven to extinction. The difficulty lies in deciding how to evaluate whether forests devoid or greatly reduced of whitebark pines due to human-driven invasive species and climate change would have more wildness value than forests populated by biotech whitebark pines.

Biotechnology and the Intrinsic Value of Forest Species, Ecosystems, and Biodiversity

Many environmental philosophers, conservationists, and conservation biologists claim that species (e.g., Soulé, 1985; Rolston, 1988; Smith, 2016), ecosystems (e.g., Leopold, 1949; Callicott, 1989), and biological diversity (Soulé, 1985; UN, 1992) have intrinsic value. These claims may have different justifications. For instance, it may be argued that species' intrinsic value rests on their long evolutionary history and potential (Soulé, 1985), or alternatively rests on the grounds that species have interests and a good of their own that are of moral significance and should be respected (Johnson, 1991). Although such claims are contested and controversial (Sandler, 2012), they are likely to feature in future debates about the use of biotechnology in forests, alongside discussions of ecosystem services.

These value positions suggest that at least some uses of biotechnology to protect or promote forest health are likely to be viewed by some constituents as positively impacting or enhancing intrinsic value. The use of biotechnology to restore the American chestnut, for example, could be understood as protecting both the intrinsic value of this species and forest ecosystems by improving their health, and also as promoting intrinsically valuable forest biodiversity by reintroducing a species on which a wide variety of other organisms depend (Powell, 2016). Similar arguments might be made for the other tree species on which the committee has focused in this report. Positive interpretations of this kind are supported by Needham and colleagues' (2016) finding that having a stronger biocentric or environmental value orientation tended to underpin a more positive attitude toward the use of biotechnology to help restore American chestnut forests.

However, this should not be taken to imply general acceptance of the use of biotechnology to promote forest health. In some cases, an application of biotechnology could present risks to certain intrinsic values, even as it protects other values. For instance, the use of biotechnology in a tree species to protect it against an invasive insect might threaten the survival of other native or endemic insect species. In addition, those who defend the intrinsic value of species, ecosystems, or biodiversity may *also* accept the intrinsic value of naturalness or wildness (Leopold, 1949; Soulé, 1985), meaning that the use of biotechnology for forest health could entail choosing *between* environmental values such as species preservation and wildness protection. Given that the use of biotechnology in forests may undermine some values while enhancing others, each possible use of biotechnology in forests is likely to need its own individual ethical case analysis (Sandler, 2018).

This potential choice brings into focus a set of broader social and ethical debates about the use of new technologies in environmental conservation. The pervasiveness of ecological impacts from forces such as climate change and invasive species means that traditional conservation strategies, including setting aside nature reserves and restoring species to habitats within their historic ranges, become significantly less likely to achieve goals such as species protection (Minteer and Collins, 2012; Sandler, 2013, 2018). To protect species and reduce biodiversity loss may then require new interventionist and managerial conservation strategies, such as the use of biotechnology. In addition to potentially negatively impacting perceptions of wildness, the use of such new technologies changes the nature of traditional conservation practices, thus raising a variety of challenges about the broader social influences of technology.

Challenges Raised by Broader Social Influences of Biotechnology

Biotechnologies developed to protect and promote forest health target particular genes in specific species for particular purposes. Although these targets may be specific and narrow, many social scientists have argued that the uses of new technologies almost always have much wider social and cultural impacts than their immediate target (Johnson and Wetmore, 2009; Slovic, 2010). Winner (2010:6) maintains that “technologies are not merely aids to human activity, but also powerful forces acting to reshape that activity and its meaning.” Technologies such as the automobile or the cellular telephone transformed societies as they were adopted, changing people’s sense of identity, the nature of human relationships and interactions, the nature of and access to employment, and people’s everyday habits. Likewise, the use of biotechnology for conservation purposes could have much broader societal effects, including the potential for reshaping some conservation purposes and practices, effects less likely to follow from the use of more traditional techniques such as tree breeding. For instance, the use of biotechnology for conservation purposes could promote a shift in the focus of conservation from more traditional calls to change human behaviors in the environment, or attempts to separate places and species from undue human impacts (e.g., by creating nature reserves), to much more managerial and interventionist strategies involving altering species and ecosystems to better fit into a human adapted world (Gamborg and Sandøe, 2010; Sandler, 2018). One particular concern here is that the use of biotechnology for forest health could have the effect of making the adoption of biotechnology seem more routine, thus serving as a perceived portal or “Trojan horse” for future biotech modifications in forests or other environments for very different—and less altruistic—purposes (Smolker, 2018).

Scholars in the social studies of science and technology have focused on processes and potential institutions to understand such potential and complex impacts through innovations in:

- Anticipatory governance (e.g., Sarewitz, 2011; Guston, 2014),
- Responsible research and innovation (e.g., Owen et al., 2012; Stilgoe et al., 2013),
- Future studies (e.g., Selin et al., 2017), and
- Deliberative public engagement (e.g., Delborne et al., 2013; Rask and Worthington, 2015; Tomblin et al., 2017).

Such processes may include attention to risks and benefits—the primary focus of U.S. regulatory oversight of biotech plants—but also expand to consider a much broader and diverse set of values in the context of uncertainty.

Social Justice Considerations in the Use of Biotechnology for Forest Health

The use of biotechnology for forest health also potentially raises social justice challenges, which may be overshadowed by analyses focusing on the services that forest ecosystems provide, rather than how the benefits, costs, and risks derived from those services are *distributed*. These social justice challenges relate to (1) *distributive justice*, defined as “the political processes and structures that affect the distribution of

benefits and burdens in societies” (Lamont and Favor, 2017); and (2) *procedural justice*, defined as “the justice of the procedures that might be used to determine how benefits and burdens of various kinds are allocated to people” (Miller, 2017). Given that the use of biotechnology in forests affects the future of forests—and therefore of humans—over the long term, social justice challenges also extend beyond present generations to include future generations, raising *intergenerational justice* challenges as well.

Distributive Justice. The use of biotechnology in forests raises possible issues of distributive justice. The most obvious justice concerns are likely to be raised where some individuals or groups bear a disproportionate share of the risks or harms from the use of biotechnology in forests, but receive few or no benefits. “Risks” and “harms” here do not primarily refer to risks to human health; relevant risks, for example, could be to the livelihood or cultural practices of forest-dependent communities. If the use of biotechnology in noncommercial forests reduced tourism, there might be a negative impact on those who depend on tourism for their livelihood (though possibly no worse than if the forest were severely affected by an insect or pathogen). Alternatively, stakeholders seeking to restore a tree species such as the American chestnut might benefit from the introduction of blight-resistant transgenic American chestnut trees, whereas stakeholders who view any genetic modification of a forest species as reducing its wildness will bear the harm. In this particular example, perceptions and values drive the distribution of harm and benefit more so than geography, race, or class.

Indigenous populations who have spiritual relationships with, and value for, particular forests and tree species are likely to be significantly affected by the use of biotechnology in noncommercial forests (Nilausen et al., 2016; see also Box 4-1). For example, black ash (*Fraxinus nigra*) has special significance for indigenous peoples in the Great Lakes region, especially for basket making (Poland et al., 2017). Although black ash is seriously threatened by the emerald ash borer, the use of biotechnology to increase resistance in black ash trees might significantly change the relationship indigenous peoples have to this species. Relatedly, recent research on the potential restoration of the American chestnut tree draws on interviews with Haudenosaunee community members and participant observation of tribal meetings. Barnhill-Dilling (2018) acknowledged great diversity in perspectives among the indigenous people with whom she interacted, but reports several themes relevant to this discussion; the committee heard similar information in one of its webinars (Dockry, 2018; McManama, 2018; Patterson, 2018). First, traditions of nonintervention in natural processes (Nelson, 2008) question the wisdom of attempting to counteract the effects of the chestnut blight altogether. Second, cultural and medicinal practices that used to involve the American chestnut tree are viewed as unlikely to be restored with a transgenic or hybrid tree. Third, disrespect and abuse of native peoples by Western scientists (Sikes, 2006; Smith, 2013) has created a culture of mistrust that fosters skepticism of scientific innovations even when they are presented as beneficial. Fourth, in a period of increased attention to indigenous cultural restoration, a narrow focus on the restoration of a single tree species is experienced by some tribal members as marginal, if not irrelevant (also see Higgs, 2005; Kimmerer, 2011). Fifth, and most broadly, in some indigenous communities, genetic engineering has come to be viewed as violating tribal sovereignty, self-determination, and the natural order (also see Harry, 2001; Roberts, 2005; Antoine, 2014; Francis, 2015; IEN, 2016) and, as noted in Box 4-1, might be interpreted as violating indigenous peoples’ rights. However, it is important not to overgeneralize. Barnhill-Dilling (2018) also reported that some indigenous representatives see chestnut blight as a destructive force and welcome the potential for a transgenic tree to restore both ecological integrity and cultural practices related to woodworking and eating chestnuts. Thus, the distribution of risks and benefits across cultural, social, and sovereign boundaries introduces great complexity in considering the social justice dimensions of forest biotechnology.

Distributive justice presents the challenge not only of considering potential risks, harms, and benefits from the use of biotechnology in forests, but also examines the ways in which those risks, harms, and benefits are distributed across populations and individuals. However, it is also important to note that the existing threat—such as from new insect pests or pathogens—to which any proposed biotechnology is responding also generates risks, harms, and benefits (e.g., employment from thinning diseased forests or a new desired species composition after the pest has gone through the forest) distributed unevenly across

populations and individuals. There is not a no-risk scenario for the cases in which biotechnology use is being considered.

Procedural Justice. The challenge of procedural justice is to ensure that those who are likely to be affected meaningfully participate in decision making about the use of biotechnology in forests; this requires inclusiveness in consultation and decision-making procedures. Including all those who are likely to be affected generates particular challenges in the case of a modification that is designed to spread in the environment and across social and political boundaries. Biotechnology used in one forest is eventually likely to reach forests (and those living in, dependent on, or visiting those forests) at a considerable distance from where trees were initially planted. Therefore, consulting only those people local to a particular proposed biotechnological use appears to be too limited.

Procedural justice also requires recognition of the standing of particular cultural groups who will be affected. For example, indigenous groups should be meaningfully and fairly included in consultations about uses of biotechnology that may affect their forests, in ways that allow for the sharing of indigenous knowledge (McGregor, 2002), recognize tribal sovereignty, cultural practices and values, even where those values diverge from the values of other communities and individuals who may also be affected (Barnhill-Dilling, 2018). Consultation is already required if federal policies affect indigenous communities (see the example in Box 6-1).⁸

Attending to procedural justice is not a recipe for avoiding controversy. In fact, expanding the number of individuals and groups meaningfully consulted is unlikely to make consensus any easier to achieve. There will likely be objections to any decisions ultimately taken. However, ensuring procedural justice allows those with authority to explain how and why particular values were prioritized, how the steps toward decision making in each case were made, and who was responsible for them, therefore displaying transparency in the decision-making procedure. Put simply, procedural justice helps ensure fairness even if outcomes are unlikely to satisfy all members of various publics.

Intergenerational Justice. Concerns about social justice extend beyond those currently alive to include future generations of human beings. Many tree species are long-lived, with life spans exceeding many human generations. Whitebark pines, for instance, do not reach reproductive age until they are at least 20 years old, may not reach maximum cone production until they are 100, and can live for more than 1,000 years. The use of biotechnology in trees that are likely to outlive those who planted them, and that will affect the species composition of forests for centuries, clearly has implications for future generations. In terms of distributive justice, if present generations could be expected to benefit from the use of biotechnology in forests, whereas future generations bore a disproportionate share of the risks and costs, this would present an issue of intergenerational injustice. However, the benefits, risks, and costs may not split this way at all; it is plausible that present generations would bear the costs of developing, breeding, and planting trees generated using biotechnology, whereas future generations would benefit from the resulting mature trees and healthy forests.

This issue is particularly challenging given the uncertainties of the effects of biotechnology over long timescales, limited knowledge about the future trajectories of current and new forest pests and climate change, and the fact that future generations cannot directly be consulted about their values and preferences with respect to the use of biotechnology. In the language of procedural justice, it is difficult to imagine a procedure that integrates the perspectives and concerns of publics of the future, although a number of ways of integrating such concerns into democratic systems have been proposed (e.g. Thompson, 2010; González-Ricoy and Gosseries, 2016).

Many other human impacts on the environment will affect things over the long term, not just the use of biotechnology in forests. Tree species have approached extinction in the past due to new pests and have recovered (Booth et al., 2012). It is possible that, in some respects, the use of biotechnology for forest health

⁸Examples of consultation models and practices with indigenous communities include Whyte et al. (2014), Farley et al. (2015), and Norton-Smith (2016).

would make less of a long-term impact than the extirpation of populations or even species extinction that could have been averted by the use of such technology. However, the long-term nature of this form of biotechnology is highlighted by the transformation of such long-lived organisms as trees (in comparison with the planting of annual crops, for instance). Frameworks that focus on “sustainability,” or the preservation of options for future generations may offer instructive insight (e.g., Hauser et al., 2014).

CONCLUSIONS AND RECOMMENDATIONS

Because trees are long-lived species that often exist in minimally managed or unmanaged environments, there are a number of ecological, economic, social, and ethical considerations that pertain to the use of biotechnology in forest trees that are not as applicable to other biotech products, such as agricultural crops. To be an effective tool in the mitigation of forest health threats, these various considerations need to be taken into account when making decisions about the deployment of a tree with biotech resistance to insect pests or pathogens.

Conclusion: Trees with resistance introduced via biotechnology will have to survive until maturity and reproduce in order to pass resistant traits on to the next generation.

Because forest trees are in minimally managed or unmanaged environments, biotech trees with resistance to pests will have to be genetically fit in their respective environments and capable of competing with other plant species to become established. They will also have to be able to convert the resistance trait into future generations without expressing additional traits, such as high fecundity and rapid growth rate, which could lead to invasiveness.

Recommendation: Research should address whether resistance imparted to tree species through a genetic change will be sufficient to persist in trees that are expected to live for decades to centuries as progenitors of future generations.

Conclusion: The importance of managing and conserving standing genetic variation to sustain the health of forests cannot be overstated.

The postglacial expansion of tree species out of the glacial refugia has shaped genetic variation in forest populations and enabled local adaptation that appears to be pervasive in widely distributed species. In this context, it is worth considering the adaptability and vulnerability of populations under future climates. Fitzpatrick and Keller (2015) demonstrated that the vulnerability could be measured in terms of *genetic offset*, a metric that identifies populations within the species’ distribution where local adaptation (*gene × environment* relationship) is most likely to be disrupted. For example, their modeling has shown that for the widely distributed boreal tree, *Populus balsamifera*, the genetic offset is the greatest along the northern range edge (Fitzpatrick and Keller, 2015). Identifying spatial regions most vulnerable to genetic offset under future environmental conditions can therefore lead to better conservation and management practices.

Recommendation: The deployment of any biotechnological solution with the goal of preserving forest health should be preceded by developing a reasonable understanding in the target species of (a) rangewide patterns of distribution of standing genetic variation including in the putative glacial refugia, if known; (b) magnitude of local adaptation (*gene × environment* relationships); and (c) identification of spatial regions that are vulnerable to genetic offset.

Conclusion: The public sector will be best positioned to lead development of biotech trees because of the public-good aspect of forest health and the intention for the spread of a biotech tree through a forest ecosystem.

The role of the public sector (including government and nonprofit entities such as private foundations) arises out of the likelihood that the private sector will not invest in the protection of forest health because it cannot fully capture the benefits that may accrue and because it will not be able to restrict access to a tree that is released with the intention that it propagate freely. Without the expectation of market revenue sufficient to justify the costs of development, the private sector will not have sufficient incentive to invest its resources. Beyond this market failure, the justification for use of public funds arises from the nonmarket benefits of healthy forests.

Conclusion: The relatively long time required for the development of a biotech tree may adversely affect the incentive for both private- and public-sector investment.

The costs of development of a biotech tree (or, indeed, any tree bred or designed for pest resistance) will be incurred up front and the benefits will follow years later. Such a difference in the timing makes investment with a long time horizon problematic. Compared to the private sector, the public sector can have greater patience when significant public benefits are forthcoming.

Conclusion: Few studies of public attitudes toward biotechnology to address forest health threats have yet been carried out in the United States. However, there has been a small handful of studies on the topic, especially in Canada and Europe. The limited data indicate that while some individuals and groups are very concerned about possible deployment of biotechnology in forests, attitudes toward the uses of biotechnology examined in these studies are somewhat positive, especially where threats to forests are severe.

Compared to the number of studies examining societal views about the use of biotechnology in agriculture and food, there have been few studies about how people think and feel about the use of biotechnology in trees to address forest health threats. Most studies have reported that the majority of study participants supported some biotechnological approaches, which were often viewed as more acceptable than doing nothing to address severe threats to forest health.

Conclusion: Existing research indicates that public knowledge and understanding about the use of biotechnology in forests is low, suggesting that current attitudes may be unstable and liable to change with more information. The power of such information to influence attitudes is mediated by the perceived trust of the sources of information, deliberation about the topic, as well as the alignment of new information with deep value orientations.

The lack of detailed knowledge by most members of the public about biotechnology, forest health, and the biotech and nonbiotech tools that could be used to address forest health means that attitudes toward the use of biotechnology in forest trees are extremely sensitive to informational messages and vulnerable to persuasion campaigns. Information delivered by trusted knowledgeable experts (e.g., forest agencies, scientists) may influence attitudes but information campaigns, even from trusted sources, may have limited success in changing attitudes depending on people's values and value orientations.

Conclusion: Some important ethical questions raised by deploying biotechnology in noncommercial forests fall outside any evaluation of changes in ecosystem services.

The use of biotechnology may negatively affect perceptions of noncommercial forests' wildness or naturalness. Conversely, the use of biotechnology may protect forests, in terms of preventing the loss of valuable species, ecosystems, and biodiversity. It may also affect the spiritual interactions some individuals and cultural groups have with forests. In some cases, the use of biotechnology may mean that protecting one value, such as a threatened species, means sacrificing another value, such as wildness. These potential

trade-offs indicate the need for case-specific ethical management assessments that take into account the different values at stake both in any proposed use of biotechnology, or in not intervening at all.

Recommendation: More studies of societal responses to the use of biotechnology to address forest health threats in the United States are needed. Such studies might investigate (1) the responses of different social and cultural groups to the deployment of biotechnology in forests, (2) the stability and consistency of attitudes toward different applications of biotechnology in a range of circumstances, (3) differences in attitudes toward biotechnology strategies (e.g., cisgenesis, transgenesis, genome editing), (4) the relationship between deeper value orientations and attitudes toward biotechnology, and (5) how people consider trade-offs between values such as wildness and species protection.

Conclusion: The use of biotechnology for forest health, especially in noncommercial forests, raises broad questions about the social impacts of technological change on society, in particular, how conservation is understood and practiced, and how far biotechnological interventions presage a change to more interventionist management of forests.

The automobile and the cellular telephone transformed societies, and the use of biotechnology for conservation purposes could also have broad societal effects. It has the potential to reshape conservation purposes and practices; for example, it could promote a shift from calls to change human behaviors in order to save the environment, to more managerial and interventionist strategies involving altering species and ecosystems to better fit into a human-adapted world. Understanding the complex impacts on society of using biotechnology in trees in minimally managed and unmanaged environments will require more study in areas of governance and public engagement.

Conclusion: The use of biotechnology for forest health raises social justice questions, both in terms of the distribution of risks, harms, and benefits across individuals and groups through time, and in terms of the procedures used to make decisions about whether, when, and where to deploy the technology. Indigenous communities may be particularly affected by these decisions. Given the longevity of trees, the use of biotechnology for forest health (or the decision not to use it) will have significant impacts on future generations.

Distributive justice is concerned with potential risks, harms, and benefits and the ways in which those risks, harms, and benefits are distributed across populations and individuals. These concerns apply to the use of biotechnology in forests as well as to the threats posed by insect pests and pathogens to forest health. Procedural justice seeks to ensure that those who are likely to be affected meaningfully participate in decision making about the use of biotechnology in forests; this requires inclusiveness in consultation and decision-making procedures. However, it does not guarantee that all parties will be satisfied with the outcome. Intergenerational justice recognizes that concerns about social justice extend to subsequent generations, which is particularly pertinent to the use of biotechnology in trees since many trees will outlive those who create and plant parent trees with resistance to forest pests. It is difficult to predict how risks, benefits, and costs will be distributed among generations because of the uncertainties of the effects of biotechnology over long timescales, limited knowledge about the future trajectories of current and new forest pests and climate change, and the fact that future generations cannot be directly consulted about their values and preferences with respect to the use of biotechnology. This uncertainty is similar for many human impacts on the environment.

Recommendation: Respectful, deliberative, transparent, and inclusive processes of engaging with people should be developed and deployed, both to increase understanding of forest health threats and to uncover complex public responses to any potential interventions, including those involving biotechnology. These processes, which may include surveys, focus groups, town hall meetings, science

cafés, and other methods, should contribute to decision making that respects diverse sources of knowledge, values, and perspectives.

REFERENCES

- Aitken, S.N., and J.B. Bemmels. 2016. Time to get moving: Assisted gene flow of forest trees. *Evolutionary Applications* 9(1):271–290.
- Aitken, S.N., and M.C. Whitlock. 2013. Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics* 44:367–388.
- Aitken, S.N., S. Yeaman, J.A. Holiday, T. Wang, S. Curtis-McLane. 2008. Adaptation, Migration or extirpation: Climate change outcomes for tree populations. *Evolutionary Applications* 1(1):95–111.
- Alberto, F.J., S.N. Aitken, R. Alía, S.C. González-Martínez, H. Hänninen, A. Kremer, F. Lefèvre, T. Lenormand, S. Yeaman, R. Whetten, and O. Savolainen. 2013. Potential for evolutionary responses to climate change—evidence from tree populations. *Global Change Biology* 19:1645–1661.
- Antoine, D. 2014. Standing Against GMOs Is Standing for Sovereignty. Indian Country Today Media Network, March 5. Available at https://newsmaven.io/indiancountrytoday/archive/standing-against-gmos-is-standing-for-sovereignty-pICTeCjyT0yiJloCO_KT7w. Accessed September 18, 2018.
- Arnold, M.L. 1992. Natural hybridization as an evolutionary process. *Annual Review of Ecology and Systematics* 23:237–261.
- Barnhill-Dilling, S.K. 2018. Engineered Governance: Public Engagement as a Path to Inclusive Environmental Governance in Genetically Engineered Trees. Ph.D. dissertation, North Carolina State University. Available at: <https://repository.lib.ncsu.edu/handle/1840.20/35317>. Accessed November 21, 2018.
- Barnosky, C.W., P.M. Anderson, and P.J. Bartlein. 1987. The northwestern US during deglaciation; vegetational history and paleoclimatic implications. Pp. 289–321 in *North America and Adjacent Oceans During the Last Deglaciation*, Vol. 3, W.F. Ruddiman and H.E. Wright, Jr., eds. Boulder, CO: Geological Society of America.
- Barrett, R.D., and D. Schluter. 2008. Adaptation from standing genetic variation. *Trends in Ecology & Evolution* 23(1):38–44.
- BEA (U.S. Bureau of Economic Analysis). 2018. Industry Facts. Available at www.bea.gov. Accessed May 22, 2018.
- Blanke, S., F. Van Breusegem, G. De Jaeger, J. Braeckman, and M. Van Montagu. 2015. Fatal attraction: The intuitive appeal of GMO opposition. *Trends in Plant Science* 20(7):414–418.
- BLS (U.S. Bureau of Labor Statistics). 2018. Employment by Sector. Available at www.bls.gov. Accessed May 22, 2018.
- Bonan, G.B. 1999. Frost followed the plow: Impacts of deforestation on the climate of the United States. *Ecological Applications* 9(4):1305–1315.
- Booth, A., and H.M. Jacobs. 1990. Ties that bind: Native American beliefs as a foundation for environmental consciousness. *Environmental Ethics* 12(1):27–43.
- Booth, R.K., S. Brewer, M. Blaauw, T.A. Minckley, and S.T. Jackson. 2012. Decomposing the mid-Holocene *Tsuga* decline in eastern North America. *Ecology* 93(8):1841–1852.
- Bower, A.D., and S.N. Aitken. 2008. Ecological genetics and seed transfer guidelines for *Pinus albicaulis* (Pinaceae). *American Journal of Botany* 95(1):66–76.
- Boyd, J., P. Ringold, A. Krupnick, R.J. Johnston, M.A. Weber, and K. Hall. 2016. Ecosystem services indicators: Improving the linkage between biophysical and economic analysis. *International Review of Environmental and Resource Economics* 8(3–4):359–443.
- Brennan, A. and Y.S. Lo. 2016. Environmental ethics. In *The Stanford Encyclopedia of Philosophy* (winter edition), E.N. Zalta, ed. Available at <https://plato.stanford.edu/archives/win2016/entries/ethics-environmental>. Accessed April 15, 2018.
- Brockerhoff, E.G., L. Barbaro, B. Castagneyrol, D.I. Forrester, B. Gardiner, J.R. González-Olabarria, P.O.B. Lyver, N. Meurisse, A. Oxbrough, H. Taki, I.D. Thompson, F. van der Plas, and H. Jactel. 2017. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and Conservation* 26:3005–3035.
- Brossard, D., and M.C. Nisbet. 2006. Deference to scientific authority among a low information public: Understanding U.S. opinion on agricultural biotechnology. *International Journal of Public Opinion Research* 19(1):24–52.
- Brown, J.E. 1985. *The Spiritual Legacy of the American Indian*. New York: Crossroad.
- Callicott, J.B., 1989. In *Defense of the Land Ethic: Essays in Environmental Philosophy*. Albany, NY: State University of New York Press.

- Callicott, J.B., and M.P. Nelson, eds. 1998. *The Great New Wilderness Debate*. Athens, GA: University of Georgia Press.
- Cartwright, C. 2018. Whitebark pine (*Pinus albicaulis*) field screening for blister rust resistance in British Columbia: Germination results. Pp. 81–87 in *Proceedings of the IUFRO Joint Conference: Genetics of Five-Needle Pines, Rusts of Forest Trees, and Strobosphere*, A.W. Schoettle, R.A. Snieszko, and J.T. Kliejunas, eds. Fort Collins, CO: U.S. Forest Service.
- Cartwright, C., N. Ukrainetz, and M. Murray. 2016. *Whitebark Pine Field Screening for Blister Rust Resistance: Establishment Report–2015/2016*. Province of British Columbia.
- Chang, W., V.A. Lantz, and D.A. MacLean. 2009. Public attitudes about forest pest outbreaks and control: Case studies in two Canadian provinces. *Forest Ecology and Management* 257(4):1333–1343.
- Clark, J.S. 2018. Our charge: Forest health measures for evaluating risk from release of biotech trees. Presentation to the National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, February 8, Washington, DC.
- Clark, W. 2011. Clarifying the spiritual value of forests and their role in sustainable forest management. *Journal for the Study of Religion, Nature and Culture* 5(1):18–38.
- Cohen, J. 2018. Federal appeals court hears CRISPR patent dispute. *Science*, April 30. Available at <http://www.sciencemag.org/news/2018/04/federal-appeals-court-hears-crispr-patent-dispute>. Accessed September 18, 2018.
- Connor, M., and M. Siegrist. 2010. Factors influencing people's acceptance of gene technology: The role of knowledge, health expectations, naturalness, and social trust. *Science Communication* 32(4):514–538.
- Cooper, N., E. Brady, H. Steen, and R. Bryce. 2016. Aesthetic and spiritual values of ecosystems: Recognising the ontological and axiological plurality of cultural ecosystem “services.” *Ecosystem Services* 21(Part B):218–229.
- Costa-Font, M., J.M. Gil, and W.B. Traill. 2008. Consumer acceptance, valuation of and attitudes towards genetically modified food: Review and implications for food policy. *Food Policy* 33(2):99–111.
- Costanza, R., R. de Groot, P. Sutton, S. van der Ploeg, S.J. Anderson, I. Kubiszewski, S. Farber, R.K. Turner. 2014. Changes in the global value of ecosystem services. *Global Environmental Change* 26:152–158.
- Cronon, W. 1995. The trouble with wilderness or getting back to the wrong nature. Pp. 69–90 *Uncommon Ground: Toward Reinventing Nature*, W. Cronon, ed. New York: W.W. Norton.
- Crowley, K.F., G.M. Lovett, M.A. Arthur, and K.C. Weathers. 2016. Long-term effects of pest-induced tree species change on carbon and nitrogen cycling in northeastern US forests: a modeling analysis. *Forest Ecology and Management* 372:269–290.
- Davison, A., I. Burns, and R. Schibeci. 1997. Problematic publics: A critical review of surveys of public attitudes to biotechnology. *Science, Technology, and Human Values* 22(3):317–348.
- Delborne, J.A., J. Schneider, R. Bal, S. Cozzens, and R. Worthington. 2013. Policy pathways, policy networks, and citizen deliberation: Disseminating the results of World Wide Views on Global Warming in the USA. *Science and Public Policy* 40(3):378–392.
- Delcourt, H.R., and P.A. Delcourt. 1984. Ice age haven for hardwoods. *Natural History* 84:22–28.
- DeLuca, K., and A. Demo. 2001. Imagining nature and erasing class and race: Carleton Watkins, John Muir, and the construction of wilderness. *Environmental History* 6(4):541–560.
- Denevan, W.M. 1992. The pristine myth: The landscape of the Americas. *Annals of the Association of American Geographers* 82(3):369–385.
- Dockry, M.J. 2018. Indigenous perspectives on the use of biotechnology in forests. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, March 2.
- Dumroese, R.K., M.I. Williams, J.A. Stanturf, and J.B.S. Clair. 2015. Considerations for restoring temperate forests of tomorrow: Forest restoration, assisted migration, and bioengineering. *New Forests* 46(5–6):947–964.
- Eagly, A.H., and S. Chaiken. 1993. *The Psychology of Attitudes*. Belmont, CA: Wadsworth.
- Eckert, C.G., K.E. Samis, and S.C. Loughheed. 2008. Genetic variation across species' geographical ranges: The central–marginal hypothesis and beyond. *Molecular Ecology* 17(5):1170–1188.
- Elliot, R. 1982. Faking Nature. *Inquiry* 25(1):81–93.
- Ellstrand, N.C. 1992. Gene flow by pollen: implications for plant conservation genetics. *Oikos* 63(1):77–86.
- EPA (U.S. Environmental Protection Agency). 2014. *Guidelines for Preparing Economic Analyses*. Washington, DC: EPA.
- FAO (United Nations Food and Agriculture Organization). 1998. *Economic and Environment Accounting for Forestry: Status and Current Efforts*. Rome: FAO.
- FAO. 2016. *Global Forest Resources Assessment 2015: How are the world's forests changing? Second edition*. Rome: FAO.

- Farley, C., T. Ellersick, and C. Jasper, eds. 2015. Forest Service Research and Development Tribal Engagement Roadmap. Available at <https://www.fs.fed.us/research/docs/tribal-engagement/consultation/roadmap.pdf>. Accessed November 17, 2018.
- Fourtey, A., A. Cornille, J.A. Shykoff, A. Snirc, and T. Giraud. 2017. Crop-to-wild gene flow and its fitness consequences for a wild fruit tree: Towards a comprehensive conservation strategy of the wild apple in Europe. *Evolutionary Applications* 10(2):180–188.
- Finucane, M.L., and J.L. Holup. 2005. Psychosocial and cultural factors affecting the perceived risk of genetically modified food: An overview of the literature. *Social Science and Medicine* 60(7):1603–1612.
- Fishbein, M., and I. Ajzen. 2010. Predicting and Changing Behavior: The Reasoned Action Approach. New York, NY: Psychology Press.
- Fitzpatrick, M.C., and S.R. Keller. 2015. Ecological genomics meets community-level modelling of biodiversity: Mapping the genomic landscape of current and future environmental adaptation. *Ecology Letters*, 18(1):1–16.
- Flint, C.G. 2006. Community perspectives on spruce beetle impacts on the Kenai Peninsula, Alaska. *Forest Ecology and Management* 227(3):207–218.
- Flint, C.G., B. McFarlane, and M. Müller. 2009. Human dimensions of forest disturbance by insects: An international synthesis. *Environmental Management* 43(6):1174–1186.
- Francis, A. 2015. Akwesasne moves to ban genetically modified food. Aboriginal Peoples Television Network, June 29. Available at <https://aptnnews.ca/2015/06/29/akwesasne-moves-ban-genetically-modified-food/>. Accessed November 21, 2018.
- Frewer, L.J., I.A. van der Lans, A. Fischer, M.J. Reinders, D. Menozzi, X. Zhang, I. van den Berg, and K.L. Zimmermann. 2013. Public perceptions of agri-food applications of genetic modification: A systematic review and meta-analysis. *Trends in Food Science and Technology* 30(2):142–152.
- Friedman, S.T., and G.S. Foster. 1997. Forest genetics on federal lands in the United States: Public concerns and policy responses. *Canadian Journal of Forest Research* 27(3):401–408.
- Fuller, L., M. Marzano, A. Peace, and C.P. Quine. 2016. Public acceptance of tree health management: Results of a national survey in the UK. *Environmental Science and Policy* 59(1):18–25.
- Gamborg, C., and P. Sandøe. 2010. Ethical considerations regarding genetically modified trees. Pp. 163–175 in *Forests and Genetically Modified Trees*, Y.A. El-Kassaby and J.A. Prado, eds. Rome: FAO.
- Gao, C., X. Ren, A.S. Mason, H. Liu, M. Xiao, J. Li, and D. Fu. 2014. Horizontal gene transfer in plants. *Functional & Integrative Genomics* 14(1):23–29.
- González-Ricoy, I., and A. Gosseries, eds. 2016. Institution for Future Generations. Oxford: Oxford University Press.
- Graff, G. and D. Zilberman. 2016. How the “IP-regulatory” complex affects incentives to develop socially beneficial products from agricultural genomics. Pp. 68–101 in *The Intellectual Property-Regulatory Complex: Overcoming Barriers to Innovation in Agricultural Genomics*, E. Marden, R.N. Godfrey, and R. Manion, eds. Vancouver: UBC Press.
- Gugger, P.F., C.T. Liang, V.L. Sork, P. Hodgskiss, and J.W. Wright. 2018. Applying landscape genomic tools to forest management and restoration of Hawaiian koa (*Acacia koa*) in a changing environment. *Evolutionary Applications* 11(2):231–242.
- Gupta, N., A. Fischer, and L. Frewer. 2012. Socio-psychological determinants of public acceptance of technologies: A review. *Public Understanding of Science* 21(7):782–795.
- Guston, D.H. 2014. Understanding “anticipatory governance.” *Social Studies of Science* 44(2):218–242.
- Guy, R.D. 2014. The early bud gets to warm. *New Phytologist* 202(1):7–9.
- Hajjar, R., and R.A. Kozak. 2015. Exploring public perceptions of forest adaptation strategies in Western Canada: Implications for policy-makers. *Forest Policy and Economics* 61:59–69.
- Hajjar, R., E. McGuigan, M. Moshofsky, and R.A. Kozak. 2014. Opinions on strategies for forest adaptation to future climate conditions in western Canada: Surveys of the general public and leaders of forest-dependent communities. *Canadian Journal of Forest Research* 44(12):1525–1533.
- Hall, C. 2007. GM technology in forestry: Lessons from the GM food “debate.” *International Journal of Biotechnology* 9(5):436–447.
- Hampe, A., and R.J. Petit. 2005. Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters* 8(5):461–467.
- Hamrick, J.L. 2004. Response of forest trees to global environmental changes. *Forest Ecology and Management*, 197(1–3):323–335.
- Harry, D. 2001. Biopiracy and globalization: Indigenous peoples face a new wave of colonialism. Indigenous People Council on Biocolonialism. Available at http://www.ipcb.org/publications/other_art/globalization.html. Accessed November 21, 2018.

- Harwood, C., and A. Ruuska. 2013. The personhood of trees: Living artifacts in the Upper Peninsula of Michigan. *Time and Mind* 3(2):135–157.
- Hauser, O.P., D.G. Rand, A. Peysakhovich, and M.A. Nowak. 2014. Co-operating with the future. *Nature* 511(7508):220–223.
- Hettinger, N., and B. Throop. 1999. Refocusing ecocentrism: De-emphasizing stability and defending wildness. *Environmental Ethics* 21(1):3–21.
- Higgs, E. 2005. The two-culture problem: Ecological restoration and the integration of knowledge. *Restoration Ecology* 13(1):159–164.
- Hinchee, M., C. Zhang, S. Chang, M. Cunningham, W. Hammond, and N. Nehru. 2011. Biotech Eucalyptus can sustainably address society's need for wood: The example of freeze tolerant eucalyptus in the southeastern US. *BMC Proceedings* 5(Suppl 7):124.
- Howe, G.T., S.N. Aitken, D.B. Neale, K.D. Jermstad, N.C. Wheeler, and T.H.H. Chen. 2003. From genotype to phenotype: Unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany* 81(12):1247–1266.
- IEN (Indigenous Environmental Network). 2016. GE Trees and Indigenous Lands, February 9. Available at <http://www.ienearth.org/ge-trees-and-indigenous-lands/>. Accessed November 21, 2018.
- Jepson, P.R., and I. Arakelyan. 2017a. Developing publicly acceptable tree health policy: Public perceptions of tree-breeding solutions to ash dieback among interested publics in the UK. *Forest Policy and Economics* 80:167–177.
- Jepson, P., and I. Arakelyan. 2017b. Exploring public perceptions of solutions to tree diseases in the UK: Implications for policy-makers. *Environmental Science and Policy* 76:70–77.
- Johnson, L. 1991. *A Morally Deep World*. Cambridge, UK: Cambridge University Press.
- Johnson, D.G., and J.M. Wetmore, eds. 2009. *Technology and Society: Building Our Sociotechnical Future*. Cambridge, MA: MIT Press.
- Jolley, R., T. Punke, R. Ringeisen, L. Selzer, J.D. Williams 2017. Final Report: The Blue Ribbon Commission on Forest and Forest Products Research & Development in the 21st Century. Greenville, SC: U.S. Endowment for Forestry and Communities.
- Justus, J., M. Colyvan, H. Regan, and L. Maguire. 2009. Buying into conservation: Intrinsic v. instrumental value. *Trends in Ecology and Evolution* 24(4):187–191.
- Kahan, D., H. Jenkins-Smith, and D. Braman. 2011. Cultural cognition of scientific consensus. *Journal of Risk Research* 14(2):147–174.
- Kalaitzandonakes, N., J.M. Alston, K.J. Bradford. 2007. Compliance costs for regulatory approval of new biotech crops. *Nature Biotechnology* 25(5):509–511.
- Kazana, V., L. Tsourgiannis, V. Iakovoglou, C. Stamatiou, A. Alexandrov, S. Araújo, S. Bogdan, G. Božič, R. Brus, G. Bossinger, A. Boutsimea, N. Celepirović, H. Cvrčková, M. Fladung, M. Ivanković, A. Kazaklis, P. Koutsou, Z. Luthar, P. Máchová, J. Malá, K. Mara, M. Mataruga, J. Moravcikova, D. Paffetti, J. Paiva, D. Raptis, C. Sanchez, S. Sharry, T. Salaj, M. Šijačić-Nikolić, N. Tel-Zur, I. Tsvetkov, C. Vettori, and N. Vidal. 2015. Public attitudes towards the use of transgenic forest trees: A cross-country pilot survey. *iForest* 9:344–353.
- Kazana, V., L. Tsourgiannis, V. Iakovoglou, C. Stamatiou, A. Alexandrov, S. Araújo, S. Bogdan, G. Božič, R. Brus, G. Bossinger, A. Boutsimea, N. Celepirović, H. Cvrčková, M. Fladung, M. Ivanković, A. Kazaklis, P. Koutsou, Z. Luthar, P. Máchová, J. Malá, K. Mara, M. Mataruga, J. Moravcikova, D. Paffetti, J. Paiva, D. Raptis, C. Sanchez, S. Sharry, T. Salaj, M. Šijačić-Nikolić, N. Tel-Zur, I. Tsvetkov, C. Vettori, and N. Vidal. 2016. Public knowledge and perceptions of safety issues towards the use of genetically modified forest trees: A cross-country pilot survey. Pp. 223–244 in *Biosafety of Forest Transgenic Trees: Improving the Scientific Basis for Safe Tree Development and Implementation of EU Policy Directives*, C. Vettori, F. Gallardo, H. Häggman, V. Kazana, F. Migliacci, G. Pilate, and M. Fladung, eds. Dordrecht, Netherlands: Springer.
- Katz, E. 1992. The big lie: Human restoration of nature. *Research in Philosophy and Technology* 12:231–241.
- Keller, S.R., N. Levsen, M.S. Olson, and P. Tiffin. 2012. Local adaptation in the flowering-time gene network of balsam poplar, *Populus balsamifera* L. *Molecular Biology and Evolution* 29(10):3143–3152.
- Kellstedt, P.M., S. Zahran, and A. Vedlitz. 2008. Personal efficacy, the information environment, and attitudes toward global warming and climate change in the United States. *Risk Analysis* 28(1):113–126.
- Kimmerer, R. 2011. Restoration and reciprocity: The contributions of traditional ecological knowledge. Pp. 257–276 in *Human Dimensions of Ecological Restoration: Integrating Science, Nature, and Culture*, D. Egan, E.E. Hjerpe, and J. Abrams, eds. Washington, DC: Island Press.
- Kinloch, B.B., Jr., R.A. Snieszko, and G.E. Dupper. 2003. Origin and distribution of *Cr2*, a gene for resistance to white pine blister rust in natural populations of western white pine. *Phytopathology* 93(6):691–694.

- Kinloch, B.B., Jr., R.A. Snieszko, and G.E. Dupper. 2004. Virulence gene distribution and dynamics of the white pine blister rust pathogen in western North America. *Phytopathology* 94(7):751–758.
- Kooistra, C.M., and T.E. Hall. 2014. Understanding public support for forest management and economic development options after a mountain pine beetle outbreak. *Journal of Forestry* 112(2):221–229.
- Kremer, A., O. Ronce, J.J. Robledo-Arnuncio, F. Guillaume, G. Bohrer, R. Nathan, J.R. Bridle, R. Gomulkiewicz, E.K. Klein, K. Ritland, A. Kupaninen, S. Gerber, and S. Schueler. 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters* 15(4):378–392.
- Kunda, Z. 1990. The case for motivated reasoning. *Psychological Bulletin* 108(3):480–498.
- Lamont, J., and C. Favor. 2017. Distributive justice. In *The Stanford Encyclopedia of Philosophy* (winter edition), E.N. Zalta, ed. Available at <https://plato.stanford.edu/archives/win2017/entries/justice-distributive/>. Accessed November 21, 2018.
- Leopold, A. 1949. *A Sand County Almanac*. Oxford: Oxford University Press.
- Levens, N.D., P. Tiffin, and M.S. Olson. 2012. Pleistocene speciation in the genus *Populus* (Salicaceae). *Systematic Biology* 61(3):401–412.
- Liepelt, S., R. Bialozyt, and B. Ziegenhagen. 2002. Wind-dispersed pollen mediates postglacial gene flow among refugia. *Proceedings of the National Academy of Sciences of the United States of America* 99(22):14590–14594.
- Lombardo, L. 2014. Genetic use restriction technologies: A review. *Plant Biotechnology Journal* 12(8):995–1005.
- Lorentz, K.A., and P.J. Minogue. 2015. Exotic Eucalyptus plantations in the southeastern US: Risk assessment, management and policy approaches. *Biological Invasions* 17(6):1581–1593.
- Lotterhos, K.E., and M.C. Whitlock. 2015. The relative power of genome scans to detect local adaptation depends on sampling design and statistical method. *Molecular Ecology* 24(5):1031–1046.
- Lovett, G. 2018. The risk to forest health posed by biotech-modified trees. Presentation to the National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, February 8, Washington, DC.
- Lucht, J.M. 2015. Public acceptance of plant biotechnology and GM crops. *Viruses* 7(8):4254–4281.
- Lull, R.B., and D.A. Scheufele. 2017. Understanding and overcoming fear of the unnatural in discussion of GMOs. Pp. 409–419 in *The Oxford Handbook of the Science of Science Communication*, K.H. Jamieson, D.M. Kahan, and D.A. Scheufele, eds. New York: Oxford University Press.
- Mackenzie, B.F., and B. Larson. 2010. Participation under time constraints: Landowner perceptions of rapid response to the emerald ash borer. *Society and Natural Resources* 23(10):1013–1022.
- Manel, S., and R. Holderegger. 2013. Ten years of landscape genetics. *Trends in Ecology & Evolution* 28(10):614–621.
- Manel, S., M.K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: Combining landscape ecology and population genetics. *Trends in Ecology & Evolution* 18(4):189–197.
- Manfredo, M.J., T.L. Teel, and A.D. Bright. 2004. Application of the concepts of values and attitudes in human dimensions of natural resources research. Pp. 271–282 in *Society and Natural Resources: A Summary of Knowledge*, M. Manfredo, J. Vaske, B. Bruyere, D. Field, and P. Brown, eds. Jefferson City, MO: Modern Litho.
- McLachlan, J.S., J.S. Clark, and P.S. Manos, P. S. 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86(8):2088–2098.
- McFarlane, B.L., and D. Watson. 2008. Perceptions of ecological risk associated with mountain pine beetle (*Dendroctonus ponderosae*) infestations in Banff and Kootenay National Parks of Canada. *Risk Analysis* 28(3):203–212.
- McGregor, D. 2002. Indigenous knowledge in sustainable forest management: Community-based approaches achieve greater success. *The Forestry Chronicle* 78(6):833–836.
- McLane, S.C., and S.N. Aitken. 2012. Whitebark pine (*Pinus albicaulis*) assisted migration potential: Testing establishment north of the species range. *Ecological Applications* 22(1):142–153.
- McManama, B.J. 2018. Indigenous perspective: Biotechnology versus the rights of Mother Earth. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, March 2.
- MEA (Millennium Ecosystem Assessment). 2005. *Ecosystems and Human Well-Being: Synthesis*. Washington, DC: 2005.
- Miller, D. 2017. Justice. In *The Stanford Encyclopedia of Philosophy* (fall edition), E.N. Zalta, ed. Available at <https://plato.stanford.edu/archives/fall2017/entries/justice/>. Accessed November 21, 2018.
- Minteer, B.A., and J.P. Collins. 2012. Species conservation, rapid environmental change, and ecological ethics. *Nature Education Knowledge* 3(10):14

- Montwé, D., M. Isaac-Renton, A. Hamann, and H. Spiecker. 2018. Cold adaptation recorded in tree rings highlights risks associated with climate change and assisted migration. *Nature Communications* 9(1):1574.
- Moore, K.D. 2007. In the shadow of the cedars: The spiritual values of old-growth forests. *Conservation Biology* 21(4):1120–1123.
- Müller, M., and H. Job. 2009. Managing natural disturbance in protected areas: Tourists' attitude towards the bark beetle in a German national park. *Biological Conservation* 142(2):375–383.
- NASEM (National Academies of Sciences, Engineering, and Medicine). 2016a. *Gene Drives on the Horizon: Advancing Science, Navigating Uncertainty, and Aligning Research with Public Values*. Washington, DC: The National Academies Press.
- NASEM. 2016b. *Genetically Engineered Crops: Experiences and Prospects*. Washington, DC: The National Academies Press.
- Neale, D.B., and A. Kremer. 2011. Forest tree genomics: Growing resources and applications. *Nature Reviews Genetics* 12:111–122.
- Needham, M., G. Howe, and J. Petit. 2016. *Forest Health Biotechnologies: What Are the Drivers of Public Acceptance? Interim report and preliminary findings for the Forest Health Initiative and U.S. Endowment for Forestry and Communities*. Available at https://www.foresthealthinitiative.org/resources/biotech_public_acceptance_Needham.pptx. Accessed November 21, 2018.
- Nelson, M.K., ed. 2008. *Original Instructions: Indigenous Teachings for a Sustainable Future*. Simon and Schuster.
- Nelson, M., and J.B. Callicott, eds. 2008. *The Wilderness Debate Rages On: Continuing the Great New Wilderness Debate*. Athens, GA: University of Georgia Press.
- Nelson, C.D., W.A. Powell, S.A. Merkle, J.E. Carlson, F.V. Hebard, N. Islam-Faridi, M.E. Staton, and L. Georgi. 2014. Biotechnology of trees: Chestnut. Pp. 3–35 in *Tree Biotechnology*, K.G. Ramawat, J.M. Merillon, and M.R. Ahuja, eds. Boca Raton, FL: CRC Press.
- Neumann, P.D., N.T. Krogman, and B.R. Thomas. 2007. Public perceptions of hybrid poplar plantations: Trees as an alternative crop. *International Journal of Biotechnology* 9(5):468–483.
- Newhouse, A.E., L.D. McGuigan, K.A. Baier, K.E. Valletta, W.H. Rottmann, T.J. Tschaplinski, C.A. Maynard, and W.A. Powell. 2014. Transgenic American chestnuts show enhanced blight resistance and transmit the trait to T1 progeny. *Plant Science* 228:88–97.
- Nilausen, C., N. Gélinas, and G. Bull. 2016. Perceived acceptability of implementing marker-assisted selection in the forests of British Columbia. *Forests* 7(11):286.
- Nonić, M., U. Radojević, J. Milovanović, M. Perović, and M. Šijačić-Nikolić. 2015. Comparative analysis of students' attitudes toward implementation of genetically modified trees in Serbia. *iForest* 8:714–718.
- Norton-Smith, K., K. Lynn, K. Chief, K. Cozzetto, J. Donatuto, M.H. Redsteer, L.E. Kruger, J. Maldonado, C. Viles, and K.P. Whyte. 2016. *Climate change and indigenous peoples: A synthesis of current impacts and experiences*. Portland, OR: U.S. Forest Service.
- Nowak, D.J., S. Hirabayashi, A. Bodine, and E. Greenfield. 2014. Tree and forest effects on air quality and human health in the United States. *Environmental Pollution* 193:119–129.
- NRC (National Research Council). 2002. *National Capacity in Forestry Research*. Washington, DC: National Academy Press.
- NRC. 2015. *Public Engagement on Genetically Modified Organisms: When Science and Citizens Connect. Workshop Summary*. Washington, DC: The National Academies Press.
- Olson, M.S., N. Levensen, R.Y. Soolanayakanahally, R.D. Guy, W.R. Schroeder, S.R. Keller, and P. Tiffin. 2013. The adaptive potential of *Populus balsamifera* L. to phenology requirements in a warmer global climate. *Molecular Ecology* 22(5):1214–1230.
- Omdal, D., A. Ramsey, and R. Snieszko. 2018. *Examining Genetic Variation and White Pine Blister Rust Resistance for Whitebark Pine (Pinus albicaulis): Field Trials in Washington and Oregon*. Washington Department of Natural Resources.
- Orr, H.A. 2005. The genetic theory of adaptation: A brief history. *Nature Reviews Genetics* 6(2):119.
- Oswalt, S.N., P.D. Miles, S.A. Pugh, and W.B. Smith. 2018. *Forest Resources of the United States, 2017: A Technical Document Supporting the Forest Service 2020 Update of the RPA Assessment*. Washington, DC: U.S. Forest Service.
- Owen, R., P. Macnaghten, and J. Stilgoe. 2012. Responsible research and innovation: From science in society to science for society, with society. *Science and Public Policy* 39(6):751–760.
- Patterson, N. 2018. Haudenosaunee & the TG chestnut. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, March 2.

- Pearce, D., G. Atkinson, and S. Mourato. 2006. *Cost Benefit Analysis and the Environment: Recent Developments*. Paris: Organisation for Economic Co-operation and Development.
- Peterson St-Laurent, G., S. Hagerman, and R. Kozak. 2018. What risks matter? Public views about assisted migration and other climate-adaptive reforestation strategies. *Climatic Change* 151(3–4):573–587.
- Poland, T.M., M.R. Emery, T. Ciaramitaro, E. Pigeon, and A. Pigeon. 2017. Emerald ash borer, black ash, and Native American basketmaking; Invasive insects, forest ecosystems and cultural practices. Pp. 127–140 in *Biodiversity, Conservation, and Environmental Management in the Great Lakes Basin*, E. Freedman and M. Meuzil, eds. Abingdon, UK: Routledge.
- Porth, I., and Y.A. El Kassaby. 2014. Current status of the development of genetically modified (GM) forest trees worldwide: A comparison with the development of other GM plants in agriculture. *CAB Reviews* 9(008):1–12.
- Poudyal, N.C., J.M. Bowker, and R.L. Moore. 2016. Understanding public knowledge and attitudes toward controlling hemlock woolly adelgid on public forests. *Journal of Forestry* 114(6):619–628.
- Powell, W. 2014. The American chestnut's genetic rebirth. *Scientific American* 310:68–73.
- Powell, W. 2016. New genetically engineered American chestnut will help restore the decimated, iconic tree. *The Conversation*, January 19. Available at <http://theconversation.com/new-genetically-engineered-american-chestnut-will-help-restore-the-decimated-iconic-tree-52191>. Accessed November 21, 2018.
- Pye, J.M., T.P. Holmes, J.P. Presteman, and D.N. Wear. 2011. Economic impacts of the southern pine beetle. Pp. 213–222 in *Southern Pine Beetle II*, R.N. Coulson, R.N. and K.D. Klepzig, eds. Asheville, NC: U.S. Forest Service.
- Rask, M., and R. Worthington. 2015. *Governing Biodiversity through Democratic Deliberation*. New York: Routledge.
- Reid, A.M., W.K. Chapman, and C.E. Prescott. 2016. Comparing lodgepole pine growth and disease occurrence at six Long-Term Soil Productivity (LTSP) sites in British Columbia, Canada. *Canadian Journal of Forest Research* 46(4):595–599.
- Reo, N., and L. Ogden. 2018. Anishnaabe Aki: An indigenous perspective on the global threat of invasive species. *Sustainability Science* 13(5):1443–1452.
- Rice, K.J., D.R. Gordon, J.L. Hardison, and J.M. Welker. 1993. Phenotypic variation in seedlings of a “keystone” tree species (*Quercus douglasii*): The interactive effects of acorn source and competitive environment. *Oecologia* 96(4):537–547.
- Richardson, A.O., and J.D. Palmer. 2007. Horizontal gene transfer in plants. *Journal of Experimental Botany* 58(1):1–9.
- Roberts, R.M. 2005. Walking backwards into the future: Māori views on genetically modified organisms. *Perspectives on Indigenous Knowledge*, WINHEC Journal. Available at <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.562.3006&rep=rep1&type=pdf>. Accessed November 21, 2018.
- Rokeach, M. 1973. *The Nature of Human Values*. New York: Free Press.
- Rolston, H. 1988. *Environmental Ethics: Duties to and Values in the Natural World*. Philadelphia: Temple University Press.
- Rolston, H. 1998. Aesthetic experience in forests. *Journal of Aesthetics and Art Criticism* 56(2):157–166.
- Rosenberger, R.S., E.M. White, J.D. Kline, and C. Cvitanovich. 2017. *Recreation Economic Values for Estimating Outdoor Recreation Economic Benefits from the National Forest System*. Portland, OR: U.S. Forest Service.
- Sandler, R. 2012. Intrinsic value, ecology, and conservation. *Nature Education Knowledge* 3(10):4.
- Sandler, R. 2013. Climate change and ecosystem management. *Ethics, Policy and Environment* 16(1):1–15.
- Sandler, R. 2018. Forest biotechnology: Environmental ethics perspectives. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, March 12.
- Sarewitz, D. 2011. Anticipatory governance of emerging technologies. Pp. 95–105 in *The Growing Gap Between Emerging Technologies and Legal-Ethical Oversight*, G.E. Marchant, B.R. Allenby, and J.R. Herkert, eds. Dordrecht, The Netherlands: Springer.
- Savolainen, O., and T. Pyhäjärvi. 2007. Genomic diversity in forest trees. *Current Opinion in Plant Biology* 10(2):162–167.
- Savolainen, O., T. Pyhäjärvi, and T. Knürr. 2007. Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution, and Systematics* 38:595–619.
- Scheufele, D.A. 2006. Messages and heuristics: How audiences form attitudes about emerging technologies. Pp. 20–25 in *Engaging Science: Thoughts, Deeds, Analysis and Action*, J. Turney, ed. London: The Wellcome Trust.
- Schmidtling, R.C. 2003. The southern pines during the Pleistocene. *Acta Horticulturae* 615: 203–209.
- Sedjo, R.A. 2006. *Toward Commercialization of Genetically Engineered Forests: Economic and Social Considerations*. Washington, DC: Resources for the Future.

- Sedjo, R.A. 2010. Social, legal and regulatory issues related to transgenic trees. Pp. 203–226 in *Forests and Genetically Modified Trees*, Y.A. El-Kassaby and J.A. Prado, eds. Rome: FAO.
- Selin, C., K.C. Rawlings, K. de Ridder-Vignone, J. Sadowski, C. Altamirano Allende, G. Gano, S.R. Davies, and D.H. Guston. 2017. Experiments in engagement: Designing public engagement with science and technology for capacity building. *Public Understanding of Science* 26(6):634–649.
- Semiz-Cuming, D., E.D. Kjaer, and R. Finkeldey. 2017. Gene flow of common ash (*Fraxinus excelsior* L.) in a fragmented landscape. *PLoS ONE* 12(10):e0186757.
- SFI (Sustainable Forestry Initiative). 2015. SFI policies. Section 7 in SFI 2015–2019 Standards and Rules. Available at <http://www.sfi-program.org/files/pdf/2015-2019-standards-and-rules-web-lr-pdf/>. Accessed November 23, 2018.
- Shafer, A., C.I. Cullingham, S.D. Cote, and D.W. Coltman. 2010. Of glaciers and refugia: A decade of study sheds new light on the phylogeography of northwestern North America. *Molecular Ecology* 19(21):4589–4621.
- Siipi, H. 2015. Is genetically modified food unnatural? *Journal of Agricultural and Environmental Ethics* 28(5):807–816.
- Sikes, P. 2006. Decolonizing research and methodologies: Indigenous peoples and cross-cultural contexts. *Pedagogy, Culture & Society* 14(3):349–358.
- Sjöberg, L. 2004. Principles of risk perception applied to gene technology. *EMBO Reports* 5:S47–S51.
- Slovic, P. 2000. *The Perception of Risk*. London: Earthscan.
- Slovic, P. 2010. *The Feeling of Risk: New Perspectives on Risk Perception*. New York: Earthscan.
- Smith, I. 2016. *The Intrinsic Value of Endangered Species*. New York: Routledge.
- Smith, L.T. 2013. *Decolonizing Methodologies: Research and Indigenous Peoples*. London: Zed Books Ltd.
- Smolker, R. 2018. Biotechnology and forest health. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, March 27.
- Snieszko, R.A., and J. Koch. 2017. Breeding trees resistant to insects and diseases: Putting theory into application. *Biological Invasions* 19(11):3377–3400.
- Soolanayakanahally, R.Y., R.G. Guy, S.N. Silim, E.C. Drewes, and W.R. Schroeder. 2009. Enhanced assimilation rate and water use efficiency with latitude through increased photosynthetic capacity and internal conductance in balsam poplar (*Populus balsamifera* L.). *Plant, Cell & Environment* 32(12):1821–1832.
- Soulé, M.E. 1985. What is conservation biology? *Bioscience* 35(11):727–734.
- Sork, V.L., S.N. Aitken, R.J. Dyer, A.J. Eckert, P. Legendre, and D.B. Neale. 2013. Putting the landscape into the genomics of trees: Approaches for understanding local adaptation and population responses to changing climate. *Tree Genetics & Genomes* 9(4):901–911.
- Stilgoe, J., R. Owen, and P. Macnaghten, P. 2013. Developing a framework for responsible innovation. *Research Policy* 42(9):1568–1580.
- Strauss, S.H., K.N. Jones, H. Lu, J.D. Petit, A.L. Klocko, M.G. Betts, B.J. Brosi, R.J. Fletcher Jr., and M.D. Needham. 2017. Reproductive modification in forest plantations: Impacts on biodiversity and society. *New Phytologist* 213(3):1000–1021.
- Strauss, S.H., M. Schmitt, and R. Sedjo. 2009. Forest scientist views of regulatory obstacles to research and development of transgenic forest biotechnology. *Journal of Forestry* 107(7):350–357.
- Thompson, D. 2010. Representing future generations: political presentism and democratic trusteeship, *Critical Review of International Social and Political Philosophy*, 13:1, 17–37
- Tomback, D., and P. Achuff. 2010. Blister rust and western forest biodiversity: Ecology, values and outlook for white pines. *Forest Pathology* 40(3–4):186–225.
- Tomblin, D., Z. Pirtle, M. Farooque, D. Sittenfeld, E. Mahoney, R. Worthington, and D. Guston. 2017. Integrating public deliberation into engineering systems: Participatory technology assessment of NASA’s asteroid redirect mission. *Astropolitics* 15(2):141–166.
- Tsourgiannis, L., V. Kazana, A. Karasavoglou, M. Nikolaidis, G. Florou, and P. Polychronidou. 2013. Exploring consumers’ attitudes towards wood products that could be derived from transgenic plantations in Greece. *Procedia Technology* 8:554–560.
- Tsourgiannis, L., V. Kazana, and V. Iakovoglou. 2015. Exploring the potential behavior of consumers towards transgenic forest products: The Greek experience. *iForest* 8:707–713.
- Tsourgiannis, L., V. Kazana, and V. Iakovoglou. 2016. A comparative analysis of consumers’ potential purchasing behaviour towards transgenic-derived forest products: The Greek case. Pp. 245–260 in *Biosafety of Forest Transgenic Trees: Improving the Scientific Basis for Safe Tree Development and Implementation of EU Policy Directives*, C. Vettori, F. Gallardo, H. Häggman, V. Kazana, F. Migliacci, G. Pilate, and M. Fladung, eds. Dordrecht, Netherlands: Springer.
- UN (United Nations). 1992. *Convention on Biological Diversity*. Available at <https://www.cbd.int/convention/text/default.shtml>. Accessed November 23, 2018.

- UN. 2006. Declaration on the Rights of Indigenous Peoples. Available at <https://www.ohchr.org/en/issues/ipeoples/pages/declaration.aspx>. Accessed November 24, 2018.
- U.S. Census Bureau. 2017. North American Industry Classification System. Washington, DC: U.S. Office of Management and Budget.
- USDA-FS (U.S. Department of Agriculture U.S. Forest Service). 2007. Valuing Ecosystem Services: Capturing the True Value of Nature's Capital. Available at <https://www.fs.fed.us/ecosystemservices/pdf/ecosystem-services.pdf>. Accessed November 23, 2018.
- USDA-FS. 2018. Forest Health Highlights in Washington—2017. Available at https://www.dnr.wa.gov/publications/rp_fh_2017_forest_health_highlights.pdf. Accessed December 6, 2018.
- Van Deynze, A., K.J. Bradford, H. Daniell, J.M. DiTomaso, N. Kalaitzandonakes, C. Mallory-Smith, C.N. Stewart, S.H. Strauss, and R. Van Acker. 2016. The science of gene flow in agriculture and its role in coexistence. Pp. 13–37 in *The Coexistence of Genetically Modified, Organic and Conventional Foods*, N. Kalaitzandonakes, P.W.B. Phillips, J. Wesseler, and S.J. Smyth, eds. New York: Springer.
- Vaske, J.J., and M.P. Donnelly. 1999. A value-attitude-behavior model predicting wildland preservation voting intentions. *Society and Natural Resources* 12(6):523–537.
- Vaske, J.J., and M.J. Manfredo. 2012. Social psychological considerations in wildlife management. Pp. 43–57 in *Human Dimensions of Wildlife Management*, D.J. Decker, S. Riley, and W.F. Siemer, eds. Baltimore, MD: Johns Hopkins University Press.
- Vaske, J.J., and D. Whittaker. 2004. Normative approaches to natural resources. Pp. 283–294 in *Society and Natural Resources: A Summary of Knowledge*, M. Manfredo, J. Vaske, B. Bruyere, D. Field, and P. Brown, eds. Jefferson City, MO: Modern Litho.
- Warwell, M.V. 2015. Genecology and Phenotypic Selection in Whitebark Pine (*Pinus albicaulis*) and Ponderosa Pine (*Pinus ponderosa*) Under Warm-Dry Climate. Doctor of Philosophy (Ph.D.) Dissertation, University of Minnesota. Available at https://conservancy.umn.edu/bitstream/handle/11299/180219/Warwell_umn_0130E_16397.pdf?sequence=1&isAllowed=y. Accessed December 6, 2018.
- Warwell, M.V., and R.G. Shaw. 2017. Climate-related genetic variation in a threatened tree species, *Pinus albicaulis*. *American Journal of Botany* 104(8):1205–1218.
- Warwell, M.V., and R.G. Shaw. 2018. Phenotypic selection on growth rhythm in whitebark pine under climatic conditions warmer than seed origins. *Journal of Evolutionary Biology* 31(9):1284–1299.
- Whyte, K.P., M. Dockry, W. Baule, and D. Fellman. 2014. Supporting tribal climate change adaptation planning through community participatory strategic foresight scenario development. In *Project Reports*, D. Brown, W. Baule, L. Briley, and E. Gibbons, eds. Great Lakes Integrated Sciences and Assessments (GLISA) Center. Available at http://glisa.umich.edu/media/files/projectreports/GLISA_ProjRep_Strategic-Foresight.pdf. Accessed November 17, 2018.
- Winner, L. 2010. *The Whale and the Reactor: A Search for Limits in an Age of High Technology*. Chicago: University of Chicago Press.

An Integrated Impact Assessment Framework

Having defined forest health and described the threats facing North American forests (see Chapter 2), examined the options available for mitigating these threats (see Chapter 3), and elucidated the ecological, economic, social, and ethical considerations that accompany the use of biotechnology in forests (see Chapter 4), this chapter turns to the process of evaluating the risks and benefits of interventions to address forest health. The committee has been tasked with identifying the information and analysis needed to inform a decision framework for using biotechnology in trees.

Any decision framework for assessing the potential impacts of introducing a biotech tree on forest health will need to enable evaluation of trade-offs between positive, negative, and neutral impacts and incorporate sources of uncertainty associated with those evaluations. This impact assessment approach integrates assessment of potential benefits within a traditional risk assessment framework, which includes evaluation of the potential degree and probability of harm and how to manage that harm (i.e., minimize or control adverse impacts) (NRC, 1996; EPA, 1998). In this context, the risk of loss of ecosystem services over part, or all, of a species' range is weighed against the potential to recover ecosystem services across that range with and without the biotech intervention. Therefore, both the benefits and tradeoffs of those benefits with any risk should be included in the impact assessment of a biotech tree in this context (versus, for example, assessment of biotech trees engineered only for commercial products). Such a framework could be used to evaluate any intervention aimed at improving forest health, including the use of selectively bred trees, pesticide use, or biological control.

IMPACT ASSESSMENT FRAMEWORK

The characteristics of forest health that are central to an impact assessment framework are contained within the term's definition in Chapter 2: structure, composition, processes, function, productivity, and resilience. However, given that the definition establishes a linkage between changes in ecosystems and in services that affect humans, an impact assessment framework should seek to establish causal linkages between them. The Millennium Ecosystem Assessment noted a lack of information on the details of these connections, except perhaps when considering food and water. Gaps exist, in particular, with respect to regulating, cultural, and supporting services, many of which are not traded in markets (MEA, 2005). The committee notes especially the challenges of incorporating nonmarket cultural ecosystem services, such as aesthetic experiences (Cooper et al., 2016). The committee also recognizes that the assessment of impacts to ecosystem services does not take into account noninstrumental, intrinsic values (see Chapters 2 and 4). Although assessing the impact of biotech trees on these intrinsic values is not incorporated into this decision framework, the committee recognizes the importance of these values and the likelihood that they will be prioritized by some stakeholders. In Chapter 7, the committee recommends further research into a framework that takes these values into account.

Fully informed assessment of the impacts of deploying biotech trees would include consideration of other options to protect forest health, including that of taking no action at all (see Chapter 3). For example, without intervention to control emerald ash borer (whether it be by selective breeding, pesticides, biocontrol, or biotechnology), many species of ash are certain to decline and, potentially, to face extinction. How will forest health be affected in this case? The roles that ash plays in the ecosystem may not be completely

lost with no intervention, as maples and other tree species may have functional overlap in some ecosystems. However, other impacts of the loss of the tree may not be remedied. For example, as noted in Chapter 4, black ash (*Fraxinus nigra*) has cultural value for some Native American communities (Poland et al., 2017), and its disappearance from the forest would have consequences for cultural ecosystem services. Organisms dependent on ash or on its effects on soils and other aspects of ecosystem structure and function may decline regardless of its replacement by other trees. If the potential impacts of a biotech tree on forest health are considered only in isolation, the likely consequences of taking no action may be not be fully appreciated. Historically, tree species have recovered from forest pests that drove them close to extinction, as in the case of eastern hemlock (*Tsuga canadensis*) during the mid-Holocene (Booth et al., 2012). However, at the time the committee was writing its report, forests were experiencing an increase in pest introductions (Lovett et al., 2016) and being affected by other stressors, such as climate change, pollution, and landscape fragmentation (Hansen et al., 2001; Dukes et al., 2009; Rogers et al., 2017). Thus, recovery dynamics possible in the past should not necessarily be expected to occur in the future.

Further, any restoration process requires consideration of silvicultural practices to restore trees to the landscape across their impacted range. Whether or not biotech seeds or seedlings are the propagules involved, access to appropriate sites and site preparation may have impacts on other areas of forest health. If planting into a closed canopy forest will require canopy openings, impacts of that disturbance and any maintenance of openings until saplings are sufficiently tall need to be assessed. For example, growth of American chestnut seedlings was enhanced under high light conditions and where competition was controlled with herbicides (Clark et al., 2012). Soil and canopy disturbance can increase susceptibility of other species to insect pests and pathogens, allow establishment of invasive plants, and increase soil erosion and carbon and water loss (e.g., Covington, 1981; Denslow et al., 1998; Mack et al., 2000; Gandhi and Herms, 2010). These unintended consequences can have impacts on ecosystem services that need inclusion in both the impact assessment and in any site management plan.

Ecosystem Services

As discussed in Chapter 2, ecosystem services are the goods and services that are of value to people, provided wholly, or in part, by ecosystems (Olander et al., 2015). They have been characterized by the Millennium Ecosystem Assessment as falling into the categories of provisioning, regulating, supporting, and cultural (Shvidenko et al., 2005). In 2015, EPA considered how ecosystem services could be classified to be useful in assessing how changes in ecosystems affect human welfare (EPA, 2015). Specifically, the interest was in understanding the consequences of human interventions in ecosystems. In the context of the committee's report, that intervention would be the introduction of a biotech tree into a forest ecosystem with the intent of gene flow through minimally managed, silvicultural, and urban forest systems. In other words, the intent of the intervention is for traits conferring resistance to insect pests and pathogens to become widespread.

There are a number of approaches to classifying ecosystem services, but for the purpose of assessing the potential for biotechnology to protect forest health, perhaps the best approach is to consider them in the context of human-induced change. The EPA (2015) classification is meant to enable characterization of the impacts of *change* in forest structure and functions on the provision of ecosystem services. To be effective, any changes that occur to ecosystem services must be considered holistically, not individually; all need to be accounted for since all are important and interlinked.

The National Ecosystem Services Classification System (NESCO; EPA, 2015) tracks elements of the environment through the products those elements produce, to the different ways those products are used or appreciated by humans, to the direct user or appreciator of the products. The classification system identifies the “hand-off” from ecosystems to human beings by specifying “environmental classes” and the “end-product classes” they provide (see Figure 5-1). The committee recognizes that the concept of ecosystem services has an anthropocentric focus on instrumental value and does not incorporate intrinsic value (NRC, 2005). As discussed above and in Chapter 2, the committee considers that further research is needed to develop a complementary conceptual framework that takes intrinsic values into account.

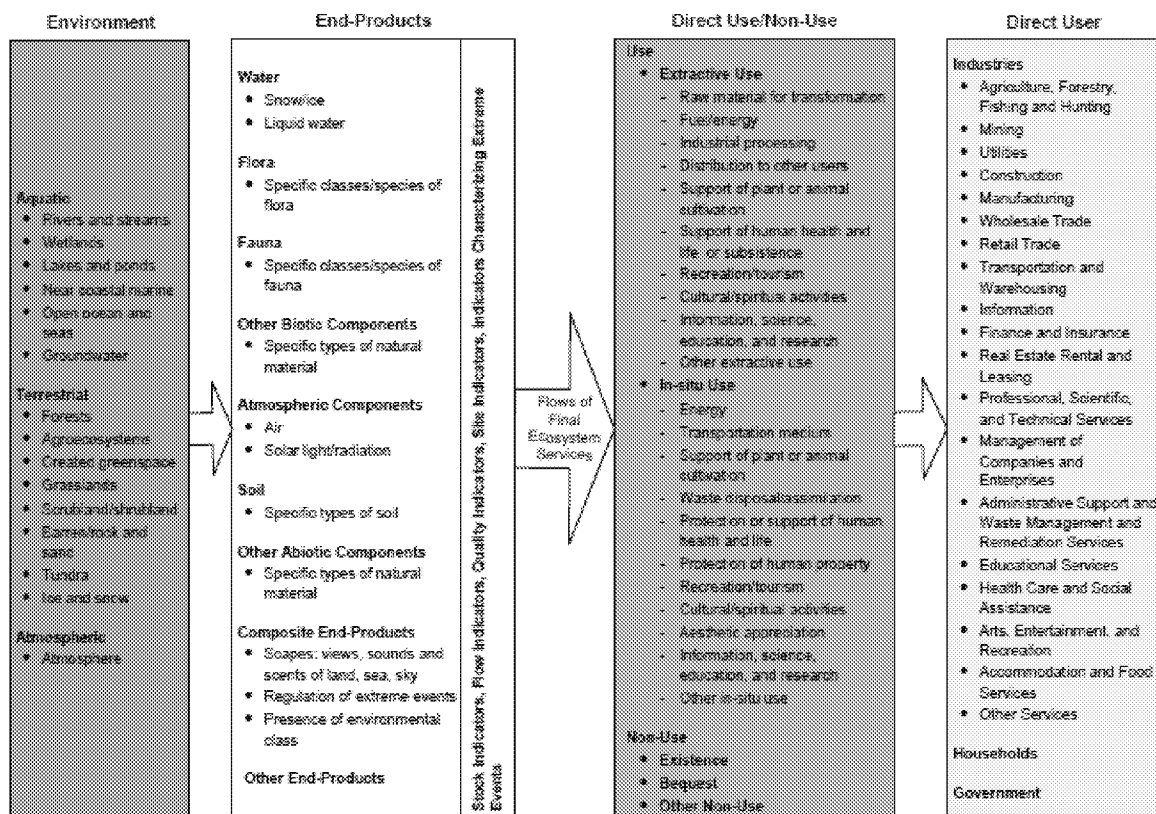


FIGURE 5-1 Four-group classification structure of the National Ecosystem Services Classification System, depicting the flow of ecosystem services from the environment to the user. NOTE: Households as Direct Users include individuals, tribes, and communities for whom cultural/spiritual activities, aesthetic appreciation, and nonuse values may be significant. SOURCE: EPA, 2015.

The NESCS (EPA, 2015) does capture the fact that not all ecosystem services are consumed by humans. Uses (consumptive and nonconsumptive) are situations in which a person actually uses a good (e.g., visits a forest), plans to use it, or entertains the possibility of using it (Pearce et al., 2006). In contrast, nonuse values are not derived from direct use or contact with ecosystems, but rather from appreciation of the existence of, say, tropical rain forests, or from a desire to preserve ecosystems for future generations (bequest value). A person could value the existence of a good (e.g., an endangered species) even though she or he may never see the good (Fisher and Turner, 2008; Cooper et al., 2016). Figure 5-1 shows the flow of services from the environment to the direct user or value for a wide range of ecosystems, including forest ecosystems.

The analysis of the impacts on human welfare based on change in ecosystem services involves identifying, quantifying, and valuing the services (EPA, 2015). The NESCS sets the stage for quantification and valuation of use and nonuse values by promoting the construction of an inclusive inventory of change. Particularly in the case of public goods associated with flows of ecosystem services, quantification may be challenging (e.g., what are the units in which scenic beauty or plant diversity is to be measured?). Valuation, as by assigning monetary values, is also complicated by the lack of market prices for services such as recharge of aquifers and clean air. At this stage, because of the challenges in quantification, cultural, aesthetic, and nonuse values may not be captured; however, the committee stresses the importance of their inclusion (see Box 5-1). There are a number of possible techniques for quantification and valuation, all of which can be problematic from a methodological standpoint (Nijnik and Miller, 2017). Ultimately, resolution of these difficulties would be needed to support impact analysis of the use of biotech trees in forests or other forest health interventions, but that analysis lies beyond the scope of this study.

BOX 5-1 Incorporating Social and Cultural Impacts

When considering interventions for forest health, the task of ensuring that impact assessment addresses social and cultural concerns is as important as the ecological impact assessment. Indeed, the social and human dimensions of the committee's definition of forest health imply the need to attend to the breadth of ecosystem services identified in this report, which include cultural and aesthetic services and nonuse values, as well as consideration of the distributional effects of changes in forest health. Engagement with affected people is key to ensuring that these impacts are identified and characterized appropriately.

Conceptually, ecosystem services are inclusive of the range of social services as represented by use and nonuse values (see Figure 5-1). However, because it is difficult to measure or quantify their values, there is potential for them to be overlooked (EPA, 2016b). As discussed in Chapter 4, social justice challenges can be overlooked by analyses that focus on the services that forest ecosystems provide rather than on how these services are distributed and who is involved in decision making about such distributions. To address environmental justice concerns requires "meaningful involvement of all people regardless of race, color, national origin or income with respect to development, implementation, and enforcement" regarding environmental policies such as the use of biotechnology in forests (EPA, 2016b:1). Public agency engagement with citizens yields opportunities for dialogue and education on both sides, in addition to providing insights into the characterization of cultural, aesthetic, and nonuse ecosystem services.

Unlike the study of potential ecological impacts of a particular intervention, social and cultural impacts cannot be calculated by experts working in isolation. Experts are required, but in a broader and more collaborative sense. For example, understanding the cultural impacts of the release of a biotech tree requires communication and engagement with multiple publics ranging from tribal groups to communities near targeted forests to conservation advocates to recreational users of forests within the range of eventual gene flow. Biotech trees in forests will slowly spread and have impacts far from where they are planted for decades or longer. Indigenous groups in the United States may be particularly affected by the use of biotechnology in forests, so consultation with them is of particular significance, as discussed in Chapter 4 (Barnhill-Dilling, 2018). Any effort to assess impacts will need to be conducted with transparency and provide ample opportunity for stakeholder participation, early on and as the assessment proceeds. Such processes may be enabled by experts as facilitators but will require the participation of individuals not always seen as experts in decision making about forest management.

Surveys of public views (e.g., attitudes, perceived risks, perceived benefits, trust) provide snapshots of information about various publics (e.g., citizens, residents, companies, agencies, nongovernmental organizations) and offer insight into estimating the social and cultural impacts of different interventions, but they have limitations (e.g., Sclove, 2010a). Given that surveys tend to offer limited context when asking questions, they do not necessarily gather *highly informed* public opinions (i.e., respondents do not have the opportunity to learn and ask questions prior to completing the survey; in contrast, see Sclove, 2010b; Rask et al., 2012; Rask and Worthington, 2015). Also, survey participants do not have an opportunity to develop their ideas in conversation with others, which is how humans often process scenarios that embody mixtures of information and values (Dietz, 2013). Finally, surveys do little to increase a sense of participation or inclusion in decision making, which can be an important issue for marginalized groups who may not trust that giving their opinions will make any difference. Yet, despite these limitations, surveys, when conducted rigorously in terms of sampling and other methodological approaches, remain an important strategy in social impact assessments by providing a rigorous and defensible method to measure relative support, prioritize concerns, or collect representative feedback from a wide array of individuals (Vaske, 2008; Dillman et al., 2014).

More deliberative processes offer an alternative strategy for contributing to social and cultural impact assessments. For example, the Danish Board of Technology pioneered "consensus conferences"—structured and facilitated groups of citizens who engaged with highly technical issues relevant to the Danish Parliament in a series of conversations and interactions with experts, culminating in reports shared with decision makers (Joss, 1998; Dryzek and Tucker, 2008). This model has been imported and adapted to the U.S. context (Guston, 1999; Kleinman et al., 2007; Bertrand et al., 2017).

(Continued)

BOX 5-1 Continued

In April 2018, faculty at North Carolina State University convened stakeholders associated with the potential deployment of the biotech American chestnut tree. The workshop emphasized the sharing of diverse perspectives, identifying decision points that could benefit from public engagement, and generating idealized engagement scenarios (Delborne et al., 2018). Benefits of such deliberative processes include:

- The potential for two-way engagement between experts and stakeholders, which promotes mutual learning and can build trust;
- A more reflective process for determining one's perspective or opinion;
- Opportunities for amplifying the concerns of marginalized groups whose perspectives may get diluted in broader survey processes; and
- The promotion of ongoing involvement that might be important to the success of long-term interventions to restore or protect forest health.

Deliberations are expensive in terms of time and resources (Kleinman et al., 2011), and they are less easily incorporated into media stories that tend to emphasize the importance of pro/con polling data (Schneider and Delborne, 2012), but they may offer rich and worthwhile insight into the generation of potential social and cultural impacts that experts alone would not identify.

At the broadest level, whatever engagement strategies are employed to identify impacts—whether opinion polling, surveys, focus groups, town hall style meetings, or science cafes (Rowe and Frewer, 2005)—the goal should be to generate high-quality information that improves decision making. Social and cultural impacts of forest management are clearly important, as evidenced by the spotted owl controversies in the Northwest (Dietrich, 1993).

The field of *social impact assessment*, which emerged in the context of evaluating potential development projects and interventions, embodies many of these perspectives.^a In a foundational article, Vanclay (2003:8) describes the breadth of social impacts to consider:

- people's way of life—that is, how they live, work, play and interact with one another on a day-to-day basis;
- their culture—that is, their shared beliefs, customs, values and language or dialect;
- their community—its cohesion, stability, character, services and facilities;
- their political systems—the extent to which people are able to participate in decisions that affect their lives, the level of democratisation that is taking place, and the resources provided for this purpose;
- their environment—the quality of the air and water people use; the availability and quality of the food they eat; the level of hazard or risk, dust and noise they are exposed to; the adequacy of sanitation, their physical safety, and their access to and control over resources;
- their health and wellbeing—health is a state of complete physical, mental, social and spiritual wellbeing and not merely the absence of disease or infirmity;
- their personal and property rights—particularly whether people are economically affected, or experience personal disadvantage which may include a violation of their civil liberties; and
- their fears and aspirations—their perceptions about their safety, their fears about the future of their community, and their aspirations for their future and the future of their children.

^aFor more details on social impact assessment, see <http://www.iaia.org>.

According to the NESCS, the effects of introducing a biotech tree would be traced to end-products (second column in Figure 5-1) and then mapped to direct uses and nonuses (see Figure 5-1, column 3) and ultimately to direct users or appreciators (see Figure 5-1, column 4). Box 5-2 describes how these effects would be traced and mapped for one of the case study trees, American chestnut. The NESCS provides an inventory of anticipated changes on which citizens and government decision makers can focus attention. Consideration of the consequences of the introduction of a biotech tree would require information not only about biotic and abiotic impacts on forest ecosystem structure and function, but also about the effect of the introduction on the availability and character of the breadth of ecosystem goods and services valued by members of society.

BOX 5-2 Ecosystem Services Framework in Practice: American Chestnut

To illustrate how the ecosystem services framework described in Figure 5-1 might apply to the introduction of a biotech tree, the committee has suggested how it might be applied to the case study of a biotech American chestnut developed for restoration. This evaluation is based on the cultural, ecological, and economic role of chestnut before its decline and on an introduction scenario covering its former distributional range (Paillet, 2002; Ellison et al., 2005). The list of the end-products and services that might be changed is preliminary. A detailed evaluation would still be necessary to thoroughly assess potential change in ecosystem services. In this respect, it is worth noting that the practical development of ecosystem systems for regulatory use is in its early stages (Beaumont et al., 2017). To advance, the committee has identified key needs for interdisciplinary collaboration, assessment of uncertainty, and modeling of complex systems, among others.

Environment

- **Aquatic:** Rivers and streams
- **Terrestrial:** Forests

End-products

- **Water:** Possible changes in water chemistry due to leaves with low C:N ratio and wood with high tannin content.
- **Flora:** If introduced and actively managed, other tree species (e.g., oaks and hickories) might decline in abundance due to chestnut competition.
- **Fauna:** Species relying on mast seeding could be affected as this resource would likely increase. Aquatic macroinvertebrates could be able to use easily decomposing leaves falling into streams. Vertebrates and invertebrates reliant on plant species that may decline or shift in local abundance with corresponding shifts in other dependent species.
- **Soil:** Addition of easily decomposing litter could affect carbon and nitrogen cycling.
- **Other abiotic components:** Due to high growth rates and durable wood, ecosystems could experience an increase in carbon storage.
- **Other end products:** High-quality timber, chestnuts for human consumption, tannins for chemical feedstock, ingredients for traditional medicine.
- **Composite end products:** Changes in scenic value, restoration of organism considered functionally extinct.

Direct Use/Nonuse

- **Use:** Extractive use, such as raw material (e.g., fuel/energy for biomass), industrial processing (e.g., tannins), support of human life and subsistence, cultural/spiritual activities, information, science education, research. In situ use, such as support of wildlife, recreation/tourism, cultural/spiritual activities, aesthetic appreciation, information, science, education, and research.
- **Nonuse:** Existence of American chestnut trees (restored from functional extinction), bequest of tree to future generations, existence of biotech tree in unmanaged landscapes (e.g., views of wildness, revitalization of ecosystem).

Direct Users

- **Industries:** Forestry, hunting, fishing; construction; manufacturing; wholesale trade; retail trade; scientific services; educational services; arts and recreation.
- **Households:** Individuals and families in tribal or nontribal communities living in or near forests or visiting forests.
- **Government:** U.S. Forest Service, National Park Service, Bureau of Land Management, state and county forest managers.

The impacts of changes to ecosystem services may be beneficial or adverse, may vary in size, and may differ across different members of society. Knowledge about these impacts provides the foundation for judgments about the potential risks and benefits of introducing a biotech tree. However, the causal linkages among changes in forest ecosystems, services, and human benefits are not always well understood by the ecologists, economists, and social scientists who must collaborate on the assessment. In 2018, the National Ecosystem Services Partnership, based at Duke University, published the *Federal Resource Management and Ecosystem Services Guidebook* (National Ecosystem Services Partnership, 2018). It provides practical advice for incorporating an ecosystems approach into resource management. As summarized in a presentation to the committee (Johnston, 2018), there are three basic steps in ecosystems services analysis that must be taken considering the specific circumstances of each intervention:

1. Scoping to establish conceptual linkages among actions, ecological systems, and ecosystem services and values to different groups;
2. Assessment and quantification to formalize causal chains, identify ecosystem service indicators and ecological production functions, and quantify changes in ecosystem services; and
3. Valuation to quantify the effects on benefits (or value) realized by different beneficiary groups.

Risk Assessment Used in Tandem with Ecosystem Service Assessments

Ecological risk assessment uses science-based methods to evaluate the likelihood of adverse ecological effects resulting from particular stressors or actions (EPA, 1998). The assessment begins with problem formulation, in which risk assessors identify assessment endpoints and develop an analysis plan. Endpoints are typically biological or physical components (e.g., abundance of species) within the environment that may be affected by the proposed action. For example, EPA (1998:26903) defines an assessment endpoint as “an explicit expression of the environmental value to be protected, operationally defined as an ecological entity and its attributes.” Particular endpoints are situationally identified based on ecological relevance, susceptibility (sensitivity to the probable exposure), and significance to management goals (EPA, 1998). The choice of appropriate endpoints is crucial in ensuring that an assessment is useful for risk managers in making effective and defensible decisions (EPA, 1998).

In 2003, EPA released a set of conventional generic ecological assessment endpoints (conventional endpoints) that are broadly applicable in many ecological contexts and harmonized with environmental legislation and EPA policy (Munns et al., 2016). Conventional endpoints are designed to directly protect ecosystem function and biodiversity and to provide science-based proxies upon which an assessment (and decisions) can be based. Proxies are necessary because not all organisms and processes in an ecosystem can be studied or monitored (Suter, 2000). Protections recommended by risk assessments focus on protecting specific aspects and organisms within an environment, but they also indirectly support and protect many ecosystem services important to humans. As such, these endpoints address many of the ecosystem services relevant to assessment of forest health. As stated above, this approach can be adopted as part of an impact assessment framework but would need refinement to incorporate the full suite of services intended in the committee’s definition of forest health.

When considering impact assessment for the use of biotechnology in forests, links between specific forest protections and their effects on important ecosystem services should be made explicit. As suggested above, the advantage of bringing ecosystem services into impact assessments is that it opens up the possibility of including a broader range of values and making the connection between the protection of forests and human well-being clear for the public, stakeholders, and policy makers (Munns et al., 2016).

Efforts to incorporate ecosystem services directly into risk assessment frameworks have been made, both to implement broader protections and to garner better public and policy maker understanding and support (EPA, 2015). EPA has adopted this approach, defining ecosystem services as the outputs of ecological functions or processes that contribute to social welfare or have the potential to do so in the future

(EPA, 2006). In 2015, EPA began explicitly encouraging the incorporation of ecosystem services into risk frameworks and released a list of ecosystem service generic assessment endpoints (ecosystem service endpoints). Because the definitions of these endpoints are intentionally broad in guidance, they must be specifically defined in individual assessments (EPA, 2015).

It is important to note that conventional and ecosystem service endpoints are complementary rather than competing concepts (see Table 5-1; EPA, 2015; Munns et al., 2016). The consideration of conventional endpoints may be legally required, and they represent the ecologically important and susceptible entities and attributes that require protection under current laws and regulations (see Chapter 6). However, although EPA considers conventional endpoints sufficient for use in risk assessment (EPA, 2015), the complexities associated with biotechnology suggest that ecosystem service endpoints should be a required component of a broader impact assessment. This approach is consistent with EPA's recommendation that ecosystem service endpoints be added in situations that need better monitoring of the effects of proposed actions on those ecosystem attributes that directly influence humans and where benefits accruing to humans from implementing protections that are not immediately obvious (EPA, 2015).

The use of ecosystem service endpoints alone may not afford sufficient protection of a forest ecosystem from the effects of intervention, because it could create a situation with perverse incentives when, in fact, the opposite was intended by the decision framework. For example, some ecosystem services may increase as an ecosystem is increasingly exploited (at least to a point), whereas some ecosystem services may decrease when protections are implemented. Therefore, the use of both conventional and ecosystem service endpoints, in tandem, may work best to produce a framework that accounts for both human use and nonuse ecosystem services and long-term ecosystem function.

EPA has considered how conventional risk assessment endpoints can be related to generic ecological assessment endpoints and then to possible generic ecosystem service assessment endpoints (EPA, 2016a). Although not customized to the current setting of development of a biotech tree, this overview may be helpful in understanding how risk assessment and ecosystem services can be integrated for use in forest ecosystems.

TABLE 5-1 Comparison of Selected Ecological and Ecosystem Service Endpoints

Conventional Ecological Assessment Endpoint	Generic Ecological Assessment Endpoint	Possible Generic Ecosystem Services Endpoint
Population abundance Population size and structure Presence/absence of game species Taxa richness	Population and abundance	Food production
Plant community uptake and deposition of pollutants	Ecosystem function	Air purification (for breathing and visibility)
Plant community net production Carbon sequestration	Ecosystem function	Climate stabilization
Water retention	Ecosystem function	Flood and storm surge regulation
Wilderness quality Endangered species and habitat area and quality	Area or quality of ecosystem or special place	Provision of aesthetic, scientific, recreational, educational, cultural, medical, genetic, ornamental, and spiritual resources

SOURCE: Adapted from Table 3 in EPA, 2016a.

The incorporation of ecosystem service endpoints, however, is not straightforward. Conventional endpoints are based on precedent, regulations, and established practices and usually have recognized metrics for assessment (EPA, 2015). They are specifically defined for each individual framework, and elements that are not applicable can be dropped and novel endpoints added when appropriate (EPA, 2015). In contrast, ecosystem service endpoints often lack foundational bases and functional metrics. Some quantitative methods exist for their estimation, but additional research will need to be conducted before they can be put into common use (Kremen, 2005; EPA, 2016a). In addition, the complexity of using ecosystem service endpoints is increased because a wide range of nonuses are taken into account (EPA, 2016a). Given that this committee's definition of forest health includes both ecological and human dimensions, explicit incorporation of both dimensions should be included in assessments of the risks, benefits, and costs of a forest health intervention, including the development and release of biotech trees.

TOOLS AVAILABLE TO INFORM AN IMPACT ASSESSMENT FRAMEWORK

Little information exists on the impacts of releasing biotech trees into minimally managed or unmanaged systems, even for those efforts with impacts likely to be similar to those of trees developed through selective breeding (Hoenicka and Fladung, 2006). Therefore, this section discusses the types of quantitative and qualitative data that will be needed, how the data can be generated, and how they can be used to inform the impact assessment approach proposed. In the case of forest trees, data on gene flow, establishment, and any potential impact of the modified tree species on the remaining forest ecosystem are critical to assessing any potential benefits and risks of implementing this technique. In many cases, the requisite information will take years to decades to compile, and often a combination of approaches will be needed to fulfill all the demands of a multidimensional assessment framework. For example, field trials evaluating biotech trees can provide information about the growth and resistance of the trees, but they can take years to develop and alone will not be sufficient for assessing the impacts of releasing the biotech tree to address forest health. However, data from field trials can be combined with data derived from other types of plant releases to parameterize simulation models to inform impact assessment. Similar modeling approaches can allow inclusion of gene flow and climatic tolerances. Models should be reassessed as specific data are obtained from field trials, allowing adaptive management of the risk assessment process. Additionally, the results of surveys and stakeholder engagement as described in Chapter 4 and Box 5-1 will provide information about human values and concerns associated with specific products of biotechnology.

Field Trials

The long-lived nature of tree species not only complicates the development and deployment of releasing biotech trees to maintain or improve forest health as described in Chapter 3, but it also makes the assessment of potential impacts difficult. Although modeling can help address the long temporal and large spatial scales involved (see the next section, "Scenario Modeling"), the question of how long to monitor the potential impacts of a genetic change in a long-lived organism and its surrounding ecosystem remains uncertain. Furthermore, even if critical unexpected impacts emerge, reversing continued gene flow will likely be impossible.

Therefore, field trials of biotech trees are a vital tool. Trials allow for an assessment of both the efficacy and the durability of resistance, and of the potential impact on the fitness of the tree species and on the ecosystems in which it will be released. The long-lived nature of trees and the varied ecosystems in which even a single tree species may occur mean the design of field trials will be more complicated and of longer duration than those currently implemented for agricultural crops. For example, many tree species do not produce significant quantities of pollen or seed for a decade or more. As in selective-breeding trials, resistance in any seedlings produced from open-pollinated seed orchards will need to be evaluated over variable environments (including areas of high disease or insect pressure) and over long time periods.

Additionally, to increase the probability that resistance to the insect pest or pathogen will spread across forested systems, field trials need to be planted in environments similar to those that the tree species will encounter. As a result, confinement conferred through climatically or geographically inhospitable environments (McDougall et al., 2011) is not an option.

One approach for assessing the suitability of the biotechnological changes and minimizing escapes may be to develop field trials within the native range of the species, but in substantial isolation from other cultivated or wild individuals in the same species or genus. In cases where this is an option, methods for tracking gene flow from seed orchards, including use of sentinel trees within and at increasing distance from orchards and planting buffer trees at edges (Scorza et al., 2013) may be useful. Simulation modeling of multiple generations will likely need to accompany field trials to better address the probability of gene flow over long time frames (Snow, 2002; Linacre and Ades, 2004; see also next section).

However, in many cases isolation will not be feasible given the long distances that pollen can travel. It is important that approaches that allow flowering and pollen production be considered carefully given that spread is virtually impossible to contain once it occurs. One advantage of tree longevity is that trial stands can be followed through the sapling stage, with removal of propagated individuals before they flower or produce cones (Häggman et al., 2013) or at the first sign of reproduction, even though in such cases there can be at least some gene flow from a few precocious trees. Short-term trials would provide time to assess for traits that might result in a harmful impact when trees are released into minimally managed or unmanaged environments. Such management has been proposed for nonnative, potentially invasive species, such as *Eucalyptus urograndis*, grown for commercial purposes (Flory et al., 2012). If permitted under controlled conditions, field plantings would need to be conducted with sufficient assurances that plants would be removed or continuously managed once the research phase was completed. Effectiveness of this approach depends on the life history and management potential of the tree species involved. The ultimate question of how long to follow field trials for a tree species will vary by species characteristics and the genetic changes incorporated via biotechnology.

The need to be precautionary about pollen production is complicated because in some cases trials would need to be of longer duration to fully assess resistance. Trees may need to be on site for many years before a pathogen has sufficient impact to judge effectiveness of breeding or biotech interventions. For example, white pine blister rust can take 5–10 years to exhibit impacts (Kinloch et al., 2008; Sniezko et al., 2012), and ash trees may need to be of sufficient size to attract pests (Duan et al., 2017). In the case of white pine blister rust, increasing pathogen abundance via increasing local abundance of the alternate host (*Ribes* spp.) may accelerate colonization of trial plantations. Thus, impact assessment will need to weigh the risk of longer-term field trials on a case-by-case basis.

Field trials are important because the potential effects of gene flow from biotech trees need serious consideration. Individuals may be in the system for decades to centuries, long after people will recall the immediate concerns that the biotechnology was intended to address, but not before the full impacts of deployment occur. Ecological, social, and cultural issues may shift over time, and it will not be possible (at least with the currently understood state of the science) to reverse decisions made in the present to address a particular threat. Gene flow can also have economic repercussions. For example, if transgenes spread into certified forest operations, this could jeopardize the certification status and its associated value; the International Forest Stewardship Council does not currently certify genetically altered tree material (Auld and Bull, 2003). Some markets may be closed to biotech trees or those that are hybrids.

Field trials will be critical to provide information about any short-term impacts and the growth, form, and resistance of the trees, but they are unlikely to provide data on interactions with other forest biota and how the release could affect the entire ecosystem. If plantation trials are successful, dispersal, establishment, and growth into mixed-species stands should also be tested in small-scale pilot plantings. Such trials would both indicate the real feasibility of the intended restoration and help parameterize models that would not only allow evaluation of whether the timing of gene flow and restoration will exceed that of species loss from the system, but also of the potential ecological impacts of the release.

Scenario Modeling

Given the long-term nature of developing a biotech tree and the limitations of field trials to fully represent long-term impacts in a forest environment, scenario modeling may prove to be a valuable tool in an impact assessment framework. Impact assessment models that use available scientific data can be developed to assess potential impacts and population dynamics. These models can be used to integrate ecological, economic, and cultural considerations, including the benefits of the proposed actions and the consequences of not carrying them out. Synthesis of all available information and data-model integration will aid in making the most accurate and informed predictions of potential impacts. Modeling gene flow after the release will also aid assessment of the success and impacts across the landscape. In addition, modeling potential scenarios that include and track sources of uncertainty will allow quantification of the reliability of the assessments, estimation of the predictive capacity of the model, and identification of data needs. However, these models, which are quantitative in nature, will be challenged by the difficulty of including many of the qualitative impacts associated with cultural considerations.

Models that simulate spread, performance, and, in some cases, impact of introduced plants are commonly developed for invasive species (e.g., Bullock et al., 2008; Ibáñez et al., 2009). These models can address different components of the invasion, including movement across the landscape (LaFleur et al., 2009; Emry et al., 2011; Marco et al., 2011), performance under different environmental conditions (Buckley et al., 2003), impacts (Rinella and Luschei, 2007; Gómez-Aparicio et al., 2008), or performance under climate change scenarios (Beaumont et al., 2009; Bradley et al., 2010). Analogous approaches could be applied to modeling the spread of biotech trees (see Box 5-3).

Data Synthesis and Data-Model Integration

Data synthesis and data-model integration are common approaches used for enhancing model realism, explanatory insight, and predictive capability (Ibáñez et al., 2014; Dietze, 2017). Data-model integration techniques can merge physiological and demographic information gathered in field trials together with known species interactions and models of gene flow to provide a broad understanding of the introduced genotype's performance under a variety of environmental conditions. Outputs from these models can provide critical information about the potential risks of releasing a new genotype into the forest by providing not only insight on the potential outcomes, but also the likelihood of the forecast.

Data synthesis and data-model integration can be implemented using multilevel, also known as hierarchical, Bayesian models (Clark, 2005). Hierarchical models can integrate diverse datasets and processes with the goal of developing predictive outcomes (Clark et al., 2010). They provide a venue for examining the complexity in a system (Clark and Gelfand, 2006). In addition, these models can incorporate new data as they become available, informing adaptive management of the biotech tree introduction. These techniques are also useful for generating forecasts under different scenarios, including climate scenarios, while still tracking the sources of uncertainty associated with the data, process, or predictor variables. Ongoing data assimilation into models will also be an important tool for continuous impact assessment and adaptive management. An iterative process of data assimilation will improve forecasts by reducing uncertainty in parameter estimates, improving model structure, and better identifying and quantifying sources of uncertainty (Luo et al., 2011).

Modeling Gene Flow

Given that biotech trees to protect forest health would be released into minimally managed or unmanaged environments, evaluation of their potential spread is critical in any impact assessment. These trees would be planted with the goal of maximizing propagule and pollen spread in ecosystems to restore a threatened species and protect or restore forest health. Along with data collected from field trials, modeling the rate of gene flow via pollen spread and seed dispersal is essential for understanding the potential spread of the introduced genes across the landscape and the necessary planting configuration. Because predicting

the impact of biotech trees released into the environment is a complex and challenging undertaking, models can also help evaluate unintended consequences of the genetic modifications on nontarget organisms and ecosystem processes.

Gene flow is a multidimensional process that is influenced by the reproductive biology of the source and recipient organisms, the disturbance and management regimes in plantations and ecosystems, climate and other abiotic factors, and the direct and indirect effects of the genetic change (Savolainen et al., 2007; Ellstrand et al., 2013; Tsatsakis et al., 2017). Given the inherent stochasticity of many of the underlying processes, as well as the large spatial and temporal scales that must be considered, direct estimation of gene flow can be quite challenging, even for well-studied annual crops with wild relatives that have relatively limited dispersal of seeds and pollen. For example, estimating transgene flow from cultivated maize to its wild relative teosinte has been highly controversial (Kinchy, 2012), due in part to the considerable methodological and sampling challenges inherent in detecting low levels of introgression over very large spatial scales (Agapito-Tenfen and Wickson, 2018). This problem is greatly magnified for trees, which are typically outcrossing, can disperse pollen and seeds over dozens or even hundreds of kilometers (Slavov et al., 2009; Williams, 2010), and may contribute pollen for centuries. This complexity means that rare, stochastic events can have outsized importance in determining gene flow rates, and these are notoriously difficult to measure (Nathan, 2006; Robledo-Arnuncio et al., 2014).

BOX 5-3 Experience from Invasion Biology

Precisely because biotech trees developed to improve forest health would be intended to spread in the environment, information from biological invasion theory can be used to inform an impact assessment. One of the mechanisms that facilitate invasion by nonnative species is that they are introduced without the natural enemies that held their populations in check in the native environment (Maron and Vilà, 2001; Keane and Crawley, 2002; Reinhart et al., 2003). Thus, increasing resistance to insects and pathogens via biotechnology that also incurs greater resistance to native insects and pathogens may create a tree that lacks the natural enemies that would otherwise keep it from outcompeting other plant species. Such changes in species competitiveness can then result in cascading effects on food webs and on the entire ecosystems (e.g., changes in nutrient cycling, disturbance regime, and hydrology) affecting the ecosystem functionality and ultimately the ecosystem services it provides (Simberloff, 2011). While this type of response is less likely if native trees are engineered to be resistant to nonnative insect pests and pathogens, the breadth of potential biotech tree development means that evaluation of this risk is necessary. Data on the competitive interactions of a biotech genotype of a species relative to nonbiotech genotypes will help to identify whether the biotech tree might become invasive.

As the traits produced by biotechnology to reduce tree vulnerability to insect pests and pathogens and to climate change are intended to spread and persist in forests, risk assessments for invasive plants can provide further guidance. The Plant Epidemiology and Risk Assessment Laboratory (PERAL) in the Center for Plant Health Science and Technology at the U.S. Department of Agriculture (USDA) Plant Protection and Quarantine program uses an approach (Koop et al., 2012) that expands on the Australian Weed Risk Assessment (AWRA; Pheloung et al., 1999). The PERAL approach addresses entry, establishment, impact, and geographic spread potential for each species assessed and includes an uncertainty analysis of the data (Koop et al., 2012). Like the impact-based AWRA (Gordon et al., 2008), the USDA Noxious Weeds Program Risk Assessment distinguished between harmful invaders and noninvaders with high accuracy in a retrospective test of introduced species (Koop et al., 2012). Additionally, the PERAL approach is relatively insensitive to the uncertainty in the data; all of the high-risk ratings and 87 percent of the low-risk ratings are corroborated by uncertainty analyses (Caton et al., 2018).

Another application of invasion biology to assessment of impacts of biotech trees is the data on the rate at which invading tree species spread. These data are most relevant for species like the American chestnut, which have been lost across some or most of their native range. In this situation, understanding the potential rate of spread may help predict recovery potential. Perhaps the best data on the lag period from date of introduction to evidence of invasion in temperate tree species indicate that it takes on average 170 years, and sometimes more than 350 years (Kowarik, 1995). As the spread of the insects and pathogens is at least an order of magnitude more rapid (Aukema et al., 2010), modeling these dynamics should assist in evaluation of the likely success of establishing a biotech tree.

A partial solution to this problem is the use of simulation modeling to integrate all of the disparate factors that affect gene flow, thereby allowing analysis of the process at spatial and temporal scales that are appropriate for biotechnology impact assessment (Ellstrand et al., 2013). While spread of small edits in native genes are difficult to track in wild populations, models can be parameterized with gene flow data from marker genes and fitness differentials from results of confined experiments.

There is some dispute about the proper time frame for such models. On one hand, simulating biotech tree establishment over many generations enables assessment of the combined effects of genetic drift and selection on abundance of resistance alleles in unmanaged or minimally managed ecosystems (Chapman and Burke, 2006; Meirmans et al., 2009). However, with trees this would require simulations that run for millennia, and the relevance of such models for near-term ecological risk assessment is questionable. Another approach is to use more detailed, spatially explicit models that run on annual time steps to allow explicit simulation of disturbance and management processes within a realistic landscape and time context (Kuparinen and Schurr, 2007; DiFazio et al., 2012). Such models allow comparison of different management and disturbance scenarios and identification of the factors that have the largest impact on spread of genes; this enables more effective prioritization of research and monitoring efforts to improve the accuracy of predictions of gene flow and evaluation of impacts.

Modeling the timing and distance of gene flow and seed dispersal could help identify the likelihood that the desired spread of the species will occur within a time frame sufficient to allow species persistence. Successful development of resistant genotypes will not confer successful species restoration if the scale of reproduction and dispersal suggests that resistant genotypes will not spread across the range of the species. Including factors associated with climate change into models may also indicate where restoration might be most successfully accomplished (Häggman et al., 2013). If changing environmental conditions suggest that the species requires planting beyond its historically native range, additional risk factors associated with this range expansion would require consideration (Aitken and Whitlock, 2013).

Limited Representation of Qualitative Impacts

Modeling is limited by its ability to incorporate factors such as social, political, cultural, and ethical issues related to the use of biotech trees to improve forest health. These factors would be incorporated if the National Ecosystem Services Classification System (EPA, 2015) were implemented (see section “Impact Assessment Framework,” above). Refinement of the ecosystem services endpoints may address some aspects (such as recreational use of a forest), but others will not be amenable to quantitative modeling (see Box 5-1).

Predictive risk assessment and modeling of the potential for sufficient spatial dispersal of the genetic change over a temporal scale to restore or recover the species should also be assessed, either within, or in analyses complementary to, those involved in assessing impacts on conventional endpoints. The predictive risk assessment would elucidate the potential for inadvertent negative genetic, ecological, or health traits to be inextricably associated with the intended positive genetic modification. If the genetic change involved has already been assessed for a crop plant species or for the species of interest in another country (e.g., biotech *Populus nigra* with insect resistance in China [FAO, 2010]), the results may inform elements of the impact assessment, as would results from selective-breeding efforts (Häggman et al., 2013). Risk assessments developed for agricultural biotech crops could help identify some of the information and analysis needs for an impact assessment framework, with the caveat that agricultural fields are much more intensively managed than noncommercial forests. Additional differences include the issues that agricultural fields are not usually viewed as “natural” environments or wilderness and that biotech crops are not planted with the intention of spread and persistence, as is intended for a biotech tree for forest health improvement.

Modeling can help elucidate the scale of potential impacts over time (e.g., Vose et al., 2015). Potential harmful invasiveness (i.e., large-scale exclusion of other native species) of the tree would be included here and might involve a modification of the USDA PERAL risk assessment (see Box 5-3). Results from confined growth trials could also inform this assessment. Although separate risk assessments for field trials

and unconfined distribution are often required for other uses of biotechnology, in this case both elements could be considered simultaneously.

Incorporating Uncertainty

Given the critical role of uncertainty analysis in risk assessment (Hayes et al., 2007), explicit evaluation of this factor should be included in the impact assessment framework (Häggman et al., 2013). Uncertainty may result from missing data, data variability, bias in the data collected, or external stochastic processes (e.g., environmental conditions). Identifying the sensitivity of the impact assessment framework to these types of uncertainty will influence both confidence in the results and the effectiveness of decision making.

There are numerous methods to evaluate uncertainty. Probabilistic models can incorporate uncertainty at all stages of the analysis (Mantyniemi et al., 2013). Even for deterministic model outputs, potential uncertainty can be assessed through expert judgment, model emulation, sensitivity analysis, temporal and spatial variability in the model output, use of multiple models, and use of statistical approaches (Uusitalo et al., 2015). As with data synthesis and data-model integration, hierarchical Bayesian models provide a useful framework for incorporating the different sources of uncertainty by representing the system as a network of components that include observed data, underlying process models, errors in parameter estimates, and models of parameter interdependence (Clark, 2005; Dietze, 2017).

Comparing outputs from different modeling approaches is a technique to offset uncertainties in the predictions (Millar et al., 2007) because they focus on different aspects of species' performances that are complementary. For example, niche models and process-based models can be combined to better predict future species performance and distribution under climate change (Morin and Thuiller, 2009; Mellert et al., 2015). Scenario modeling can also be used to assess impact of, and responses to, environmental stochasticity. Furthermore, these predictions can be improved with data as these become available over time, allowing for verification of the forecasts, improvement of management practices, and validation and reevaluation of the models. Hierarchical Bayesian models can accommodate complex processes within a spatiotemporal context and still track the uncertainty associated with each component (Wikle, 2015). These methods also allow tracking uncertainty in any forecasts generated by modeling outcomes under potential scenarios.

Impact assessment models that use available scientific information can be developed to assess potential benefits, risks, and dynamics. These assessments would integrate ecological, economic, and cultural considerations, including the impacts of the proposed actions and the consequences of not carrying them out. Synthesis of all available information will aid with making the most accurate and informed predictions of potential risks (Dietze, 2017). In addition, modeling potential scenarios that include and track sources of uncertainty will allow quantification of the reliability of the assessments, estimation of the predictive capacity of the model, and identification of data needs. However, as described above, the processes of establishment and spread of forest trees are complex and occur over large spatial and temporal spans, so even estimating the uncertainty in key parameters is challenging. A potential solution to this problem is the use of adaptive management.

USE OF ADAPTIVE MANAGEMENT

The concept of adaptive management was formalized in the 1970s as a flexible approach to natural resource management that uses data collected during implementation of a management action to evaluate the efficacy of that action and make any needed modifications (Holling, 1978; Walters and Hilborn, 1978). Multiple types of adaptive management have been identified, ranging from active to passive. As defined by Williams (2011:1371) "active adaptive management actively pursues the reduction of uncertainty through management interventions, whereas passive adaptive management focuses on resource objectives, with learning a useful but unintended by-product of decision making." Because active adaptive management is designed to identify the actions best able to meet management objectives, experimental (or quasi-experi-

mental) comparisons of management applications are employed. Monitoring of existing management efforts to conduct the assessment is more passive and generally less expensive. Because biotech trees would require new field trials (if permitted), establishing active adaptive management efforts may be less costly than using this approach for other purposes.

There is increasing interest in using adaptive management coupled with ecosystem services as a new way forward in natural resources management in the United States (Epanchin-Niell et al., 2018). The overall framework is depicted in Figure 5-2. The process begins with a “deliberative phase” during which the problem is framed by engaging the stakeholders, identifying endpoints, developing models, and deciding on an initial course of action. The procedures for defining endpoints in an ecosystem services context and developing models are discussed above (see section “Risk Assessment Used in Tandem with Ecosystem Service Assessments,” above). Next is the “iterative phase” during which the initial management actions are implemented, and outcomes are monitored to provide data about the efficacy of the management actions relative to the defined endpoints. The final phase is “institutional learning,” which requires an administrative process to evaluate the data from the technical learning phase and recalibrate endpoints and refine management as needed. This process is intended to be open-ended and iterative, where the learning cycle would continuously improve the solutions to the problem. Adaptive management has been suggested as an effective framework for managing exotic tree introductions for biofuel production (Lorentz and Minogue, 2015) as well as for release of biotech trees into the environment (Strauss et al., 2010).

The current U.S. biotechnology regulatory system accommodates adaptive management approaches associated with field trials, although this may be limited for forest trees due to restrictions on flowering (Strauss et al., 2015).¹ The committee was not asked to make recommendations about the regulatory process, but it was tasked with identifying how adaptive management can be used to enable realistic testing and assessment of biotechnology approaches for mitigating threats to forest health.

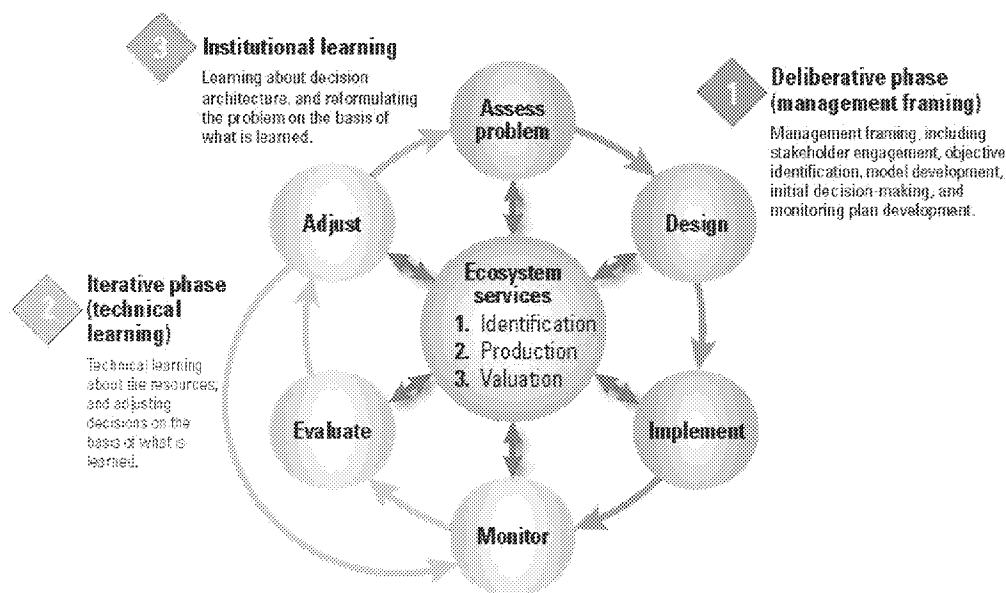


FIGURE 5-2 Model for integrating endpoint analysis based on ecosystem services with risk assessment in an adaptive management framework. SOURCE: Epanchin-Niell et al., 2018.

¹The U.S. biotechnology regulatory system for biotech plants as it relates to forest health is discussed in the next chapter. Additional detail on the regulatory system can be found in Chapter 9 of *Genetically Engineered Crops: Experiences and Prospects* (NASEM, 2016).

The 2017 National Academies report *Preparing for Future Products of Biotechnology* suggested a tiered risk assessment framework that incorporates adaptive management (NASEM, 2017). Under such a system, new biotech products are initially assessed and assigned to “bins” that are defined by the novelty and complexity of the product. Each bin then follows a different risk analysis procedure. For example, a native tree that is engineered to have increased expression of a cisgene might fall into the “familiar or noncomplex” bin. In contrast, a native tree engineered with a synthetic gene that confers levels of insect tolerance not seen in nature might fall into the “unfamiliar or complex” bin, triggering a more extensive external input process, as well as interactions between responsible federal agencies and expert advisory panels. A native tree engineered with a gene from an unrelated species introduced through *Agrobacterium* might fall somewhere in the middle because such modification is familiar, having been conducted for many years in agricultural crops, but trees with such modifications have been released only in agricultural settings rather than in minimally managed environments.

To illustrate how adaptive management might be applied in a tiered risk framework, biotech trees that fall into the lower risk bins would be good candidates for adaptive management. Such trees could be established in large field trials and allowed to flower under a streamlined permitting system. As part of the permitting process, a monitoring plan would be developed to ensure that data could be collected to reduce the uncertainty in critical parameter estimates, such as growth rates, age of flowering, gene flow distances, establishment rates, stability of resistance, occurrence of unanticipated pleiotropic effects of the genetic modification, and assessment of impacts on key ecosystem services. The data could then be used to refine simulation models to obtain more precise prediction of potential outcomes. These analyses could then be used to propose increasingly larger environmental releases until the trees are either discontinued or deregulated by USDA-APHIS. Similar adaptive management could be employed for biotech trees falling in other bins in a tiered framework. This stepwise approach may be the only practical way to obtain realistic data on gene flow and impacts at the spatial and temporal scales that are needed for proper impact assessment for biotech trees.

In 2008, the USDA Forest Service modified their procedures to integrate adaptive management into their compliance with the National Environmental Policy Act (NEPA) in 36 CFR Part 220 (USDA-FS, 2008). This adjustment allowed the Forest Service to implement initial management practices when there was some uncertainty about their impacts on desired endpoints, monitor the effects of the management practices, and then alter those practices as needed. The initial environmental assessment carried out to comply with NEPA has to clearly identify adjustments that could be made in response to monitoring in the adaptive management context.

A good example of implementation of adaptive management by the Forest Service is provided by the Black Hills Mountain Pine Beetle Response Project (USDA-FS, 2012). This project was focused on mitigating the impacts of the mountain pine beetle (*Dendroctonus ponderosae*) in the Black Hills National Forest, where an epidemic outbreak of mountain pine beetle was devastating hundreds of thousands of acres of ponderosa pine (*Pinus ponderosa*) forest. The public called for mitigating impacts of the beetles through stand management and treatment of infested trees. The main goals were to maintain biodiversity, reduce fire risks from the large amount of accumulated fuel from dead trees, and preserve the scenic beauty of the area. The proposed management intervention was an integrated pest management plan that used a decision tree (see Figure 5-3) to choose among multiple options for stand thinning, treatment of infested trees by burning or chipping, judicious use of insecticides on high value trees, and use of semiochemicals² to attract beetles to specific trees where they could be destroyed. These latter three treatments were to be conducted on a small scale initially, coupled with monitoring and assessment to determine their efficacy. These treatments would be scaled up or abandoned depending on the outcome. The project included an effectiveness monitoring plan that is implemented by project leaders and interdisciplinary resource specialists on 10 percent of the treated sites annually. The plan was developed and implemented through extensive consultation

²Semiochemicals are chemical substances or mixtures that carry information between organisms and cause changes in organisms’ behavior. In pest management, they are used to draw insects to traps for monitoring or removal purposes.

with state agencies, state government officials, tribes, conservation groups, and an advisory board comprising 16 stakeholders. As of 2018, the beetle epidemic had ended in most parts of the forest. The most recent monitoring report stated that efforts to mitigate the risk of fire to local communities from the beetle-killed trees continued and scenery objectives were on track to be met, but concerns about loss of habitat diversity in the forest prompted recommendations for approaches that would respond adaptively to those concerns (USDA-FS, 2018).

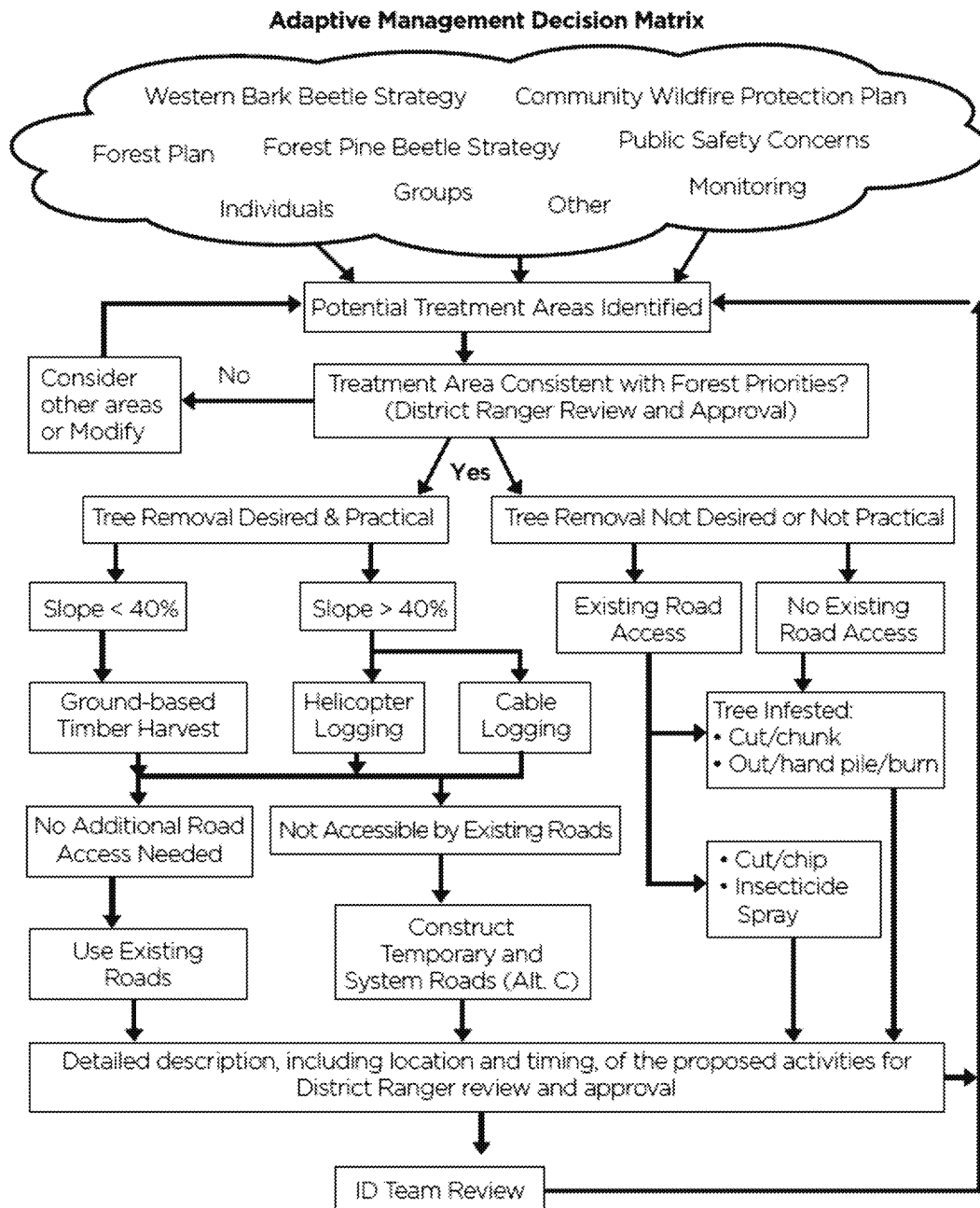


FIGURE 5-3 Adaptive management decision matrix for mountain pine beetle control in the Black Hills National Forest. SOURCE: USDA-FS, 2012.

This example illustrates the value of adaptive management in a situation where there are multiple, potentially competing endpoints and uncertainty about the impacts of management interventions. Such circumstances could also be the case for impact assessment of biotech trees modified to improve resistance to insects or diseases. There will be multiple stakeholders with potentially competing interests, and the magnitude and complexity of the problem virtually ensure a great deal of uncertainty about potential impacts of such a tree on ecosystem services. The adaptive management approach allows testing of interventions coupled with careful monitoring to both reduce the risk of unanticipated consequences and to refine the approaches to management based on learning from the initial field trials.

For example, in the case of American chestnut engineered with the oxalate oxidase transgene to resist chestnut blight, if regulators decide that the overall ecological risk is relatively low (e.g., due to extensive experience with the gene involved and the method of the genetic modification and the historic presence of the American chestnut in native forests), a plan might be developed to release engineered chestnuts on a limited basis on a small land area in consultation with stakeholders and informed by extensive simulation modeling. The plots would be monitored for key parameters that were determined by modeling to be important factors controlling the spread of chestnut. These would likely include factors such as blight resistance, growth rate, seed production, seed dispersal, seedling establishment, seedling survival, wildlife usage, soil characteristics, and overall stand biodiversity. The models could be updated with this new information and used, again in consultation with stakeholders, to either scale up the release or to terminate the established trees.

CONCLUSIONS AND RECOMMENDATIONS

Using an impact assessment framework that builds on the National Ecosystem Services Classification System developed by EPA would help those who may develop, approve, and live with biotech trees to minimize the risks of using biotechnology in forest trees while increasing the benefits to forest health. It would help identify the ecosystem services, including those related to cultural and societal values, that are important for addressing forest health within the context of each tree species being modified. Using data from field trials and results from models, impacts on the ecosystem could also be forecasted and evaluated. Adaptive management strategies to adjust the type of resistance introduced or planting decisions would also help minimize risks while increasing benefits.

Conclusion: An integrated impact assessment framework that combines ecological risk assessment with consideration of ecosystem services would provide a way to evaluate impacts of introduction of a biotech tree both on the forest functions and on the ecosystem services provided. Societal and cultural values need to be incorporated into this approach.

Impact assessment integrates assessment of potential benefits within a traditional risk assessment framework, weighing the risk of loss of ecosystem services over part, or all, of a species' range against the potential to recover ecosystem services across that range with and without the biotech intervention. Bringing ecosystem services into impact assessments improves the ability to take into account social and cultural values, which are difficult to quantify and therefore often omitted from impact assessments. It also makes the connection between the protection of forests and human well-being clearer for the public, stakeholders, and policymakers.

Recommendation: Federal agencies should continue efforts to improve the incorporation of all components of ecosystem services into the integrated impact assessment.

Conclusion: Field trials are an important tool to gather data on biotech trees in terms of gene flow, the durability and effectiveness of resistance, seed generation and dispersal, genetic fitness, and some impacts on the ecosystems into which the trees are planted.

Evaluating the success of an introduced resistance trait in trees can be difficult because of their long life spans. Furthermore, success has many dimensions: resistance to the target pest, conversion to the next generation, fitness in the environment, and lack of adverse effects on other species in the environment. Field trials create conditions for observing and measuring the degree of success in these different categories. The long-lived nature of trees and the varied ecosystems in which even a single tree species may occur mean that field trials will need to take place in many locations for a single species. Field trials are also important because of the potential effects of gene flow from biotech trees, and they also will provide information about the feasibility of using biotech trees with resistance to accomplish species restoration or preservation goals.

Conclusion: Modeling efforts will be essential to address the large spatial and temporal scales and stochastic nature of biotech tree impact assessment.

Impact assessment models that use available scientific data can integrate ecological, economic, and cultural considerations, including the benefits of the proposed actions and the consequences of not carrying them out. Synthesis of all available information, data-model integration, and modeling gene flow will aid with making the most accurate and informed predictions of potential impacts. Modeling potential scenarios that include and track sources of uncertainty will allow quantification of the reliability of the assessments, estimation of the predictive capacity of the model, and identification of data needs.

Recommendation: Modeling and other approaches should be developed to address questions about biotech tree gene flow, dispersal, establishment, performance, and impact that are precluded where flowering of field trial material is restricted.

Recommendation: Models for tree biotech impact assessments should identify, quantify, and account for sources of uncertainty.

Conclusion: Iterative decision making is required, such that impact assessments are continually modified with improvements in knowledge gained through on-the-ground experience with biotech tree development, testing, and deployment because of the uncertainty associated with predictions of the impacts of release of biotech trees into minimally managed or unmanaged environments.

As field trials return more data and models improve, the decisions based on those tools will need to be continually adjusted to ensure that steps being taken to address forest health maximize benefits and minimize risks. Impacts are likely to vary across biotech tree species and will need case-by-case evaluation.

Recommendation: An adaptive management approach to forest health should be used to ensure continued learning and address impacts both to the environment and society.

Recommendation: Impact assessment should be a continuous and iterative process.

REFERENCES

- Agapito-Tenfen, S.Z., and F. Wickson. 2018. Challenges for transgene detection in landraces and wild relatives: Learning from 15 years of debate over GM maize in Mexico. *Biodiversity and Conservation* 27(3):539–566.
- Aitken, S.N., and M.C. Whitlock. 2013. Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics* 44:367–388.
- Aukema, J.E., D.G. McCullough, B. Von Holle, A.M. Liebhold, K. Britton, and S.J. Frankel. 2010. Historical accumulation of nonindigenous forest pests in the continental United States. *BioScience* 60(11):886–897.
- Auld, G. and G.Q. Bull. 2003. The institutional design of forest certification standards initiatives and its influence on the role of science: The case of forest genetic resources. *Journal of Environmental Management* 69(1):47–62.

- Barnhill-Dilling, S.K. 2018. Engineered Governance: Public Engagement as a Path to Inclusive Environmental Governance in Genetically Engineered Trees. Ph.D. dissertation, North Carolina State University. Available at: <https://repository.lib.ncsu.edu/handle/1840.20/35317>. Accessed November 21, 2018.
- Beaumont, L.J., R.V. Gallagher, W. Thuiller, P.O. Downey, M.R. Leishman, and L. Hughes. 2009. Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions* 15(3):409–420.
- Beaumont, N.J., R. Mongrue, and T. Hooper. 2017. Practical application of the Ecosystem Service Approach (ESA): Lessons learned and recommendations for the future. *International Journal of Biodiversity Science, Ecosystem Services, and Management* 13(3):68–78.
- Bertrand, P., Z. Pirtle, and D. Tomblin. 2017. Participatory technology assessment for Mars mission planning: Public values and rationales. *Space Policy* 42(Supplement C):41–53.
- Booth, R.K., S. Brewer, M. Blaauw, T.A. Minckley, and S.T. Jackson. 2012. Decomposing the mid-Holocene *Tsuga* decline in eastern North America. *Ecology* 93(8):1841–1852.
- Bradley, B., D. Wilcove, and M. Oppenheimer. 2010. Climate change increases risk of plant invasion in the Eastern United States. *Biological Invasions* 12(6):1855–1872.
- Buckley, Y.M., D.T. Brie, and M. Rees. 2003. Demography and management of the invasive plant species *Hypericum perforatum*. II. Construction and use of an individual-based model to predict population dynamics and the effects of management strategies. *Journal of Applied Ecology* 40:494–507.
- Bullock, J.M., R.F. Pywell, and S.J. Coulson-Phillips. 2008. Managing plant population spread: Prediction and analysis using a simple model. *Ecological Applications* 18(4):945–953.
- Caton, B.P., A.L. Koop, L. Fowler, L. Newton, and L. Kohl. 2018. Quantitative uncertainty analysis for a weed risk assessment system. *Risk Analysis* 38(9):1972–1987.
- Chapman, M.A. and J.M. Burke. 2006. Letting the gene out of the bottle: The population genetics of genetically modified crops. *New Phytologist* 170(3):429–443.
- Clark, J.S. 2005. Why environmental scientists are becoming Bayesians. *Ecology Letters* 8(1):2–14.
- Clark, J.S., D. Bell, C. Chu, B. Courbaud, M. Dietze, M. Hersh, J. HilleRisLambers, I. Ibáñez, S. LaDeau, S. McMahon, J. Metcalf, J. Mohan, E. Moran, L. Pangle, S. Pearson, C. Salk, Z. Shen, D. Valle, and P. Wyckoff. 2010. High-dimensional coexistence based on individual variation: A synthesis of evidence. *Ecological Monographs* 80(4):569–608.
- Clark, J.S., and A.E. Gelfand. 2006. A future for models and data in ecology. *Trends in Ecology & Evolution* 21(7):375–380.
- Clark, S., H. McNab, D. Loftis, and S. Zarnoch. 2012. American chestnut growth and survival five years after planting in two silvicultural treatments in the southern Appalachians, USA. *Forests* 3(4):1017–1033.
- Cooper, N., E. Brady, H. Steen, and R. Bryce. 2016. Aesthetic and spiritual values of ecosystems: Recognising the ontological and axiological plurality of cultural ecosystem “services.” *Ecosystem Services* 21(Part B):218–229.
- Covington, W.W. 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology* 62(1):41–48.
- Delborne, J.A., A.R. Binder, L. Rivers, J.C. Barnes, S.K. Barnhill-Dilling, D. George, A. Kokotovich, and J. Sudweeks. 2018. Biotechnology, the American Chestnut Tree, and Public Engagement: Workshop Report. North Carolina State University, Genetic Engineering and Society Center. Available at <https://research.ncsu.edu/ges/files/2018/10/Biotech-American-Chestnut-Public-Engagement-2018.pdf>. Accessed October 29, 2018.
- Denslow, J.S., A.M. Ellison, and R.E. Sanford. 1998. Treefall gap size effects on above-and below-ground processes in a tropical wet forest. *Journal of Ecology* 86(4):597–609.
- Dietrich, W. 1993. *The Final Forest: The Battle for the Last Great Trees of the Pacific Northwest*. New York: Penguin Books.
- Dietz, T. 2013. Bringing values and deliberation to science communication. *Proceedings of the National Academy of Sciences of the United States of America* 110(Supplement 3):14081–14087.
- Dietze, M.C. 2017. *Ecological Forecasting*. Princeton, NJ: Princeton University Press.
- DiFazio, S.P., S. Leonardi, G.T. Slavov, S.L. Garman, W.T. Adams, and S.H. Strauss. 2012. Gene flow and simulation of transgene dispersal from hybrid poplar plantations. *New Phytologist* 193(4):903–15.
- Dillman, D.A., J.D. Smyth, and L.M. Christian. 2014. *Internet, Phone, Mail, and Mixed-Mode Surveys: The Tailored Design Method*. Hoboken, NJ: Wiley.
- Dryzek, J.S., and A. Tucker. 2008. Deliberative innovation to different effect: Consensus conferences in Denmark, France, and the United States. *Public Administration Review* 68(5):864–876.
- Duan, J.J., L.S. Bauer, and R.G. Van Driesche. 2017. Emerald ash borer biocontrol in ash saplings: The potential for early stage recovery of North American ash trees. *Forest Ecology and Management* 394:64–72.

- Dukes, J.S., J. Pontius, D. Orwig, J.R. Garnas, V.L. Rodgers, N. Brazee, B. Cooke, K.A. Theoharides, E.E. Stange, R. Harrington, J. Ehrenfeld, J. Gurevitch, M. Lerda, K. Stinson, R. Wick, and M. Ayres. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 39(2):231–248.
- Ellison, A.M., M.S. Bank, B.D. Clinton, E.A. Colburn, K. Elliott, C.R. Ford, D.R. Foster, B.D. Kloeppel, J.D. Knoepp, G.M. Lovett, J. Mohan, D.A. Orwig, N.L. Rodenhouse, W.V. Sobczak, K.A. Stinson, J.K. Stone, C.M. Swan, J. Thompson, B. Von Holle, and J.R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3(9):479–486.
- Ellstrand, N.C., P. Meirmans, J. Rong, D. Bartsch, A. Ghosh, T.J. de Jong, P. Haccou, B.-R. Lu, A.A. Snow, C.N. Stewart, Jr., J.L. Strasburg, P.H. van Tienderen, K. Vrieling, and D. Hooftman. 2013. Introgression of crop alleles into wild or weedy populations. *Annual Review of Ecology, Evolution, and Systematics* 44:325–345.
- Emry, D.J., H.M. Alexander, and M.K. Tourtellot. 2011. Modelling the local spread of invasive plants: Importance of including spatial distribution and detectability in management plans. *Journal of Applied Ecology* 48(6):1391–1400.
- EPA (U.S. Environmental Protection Agency). 1998. Guidelines for Ecological Risk Assessment. Federal Register 63(93):26846–26924.
- EPA. 2006. Ecological Benefits Assessment Strategic Plan. Washington, DC: EPA.
- EPA. 2015. National Ecosystem Services Classification System (NESCS): Framework Design and Policy Application. Washington, DC: EPA.
- EPA. 2016a. Ecosystem Services as Assessment Endpoints in Ecological Risk Assessment. EPA/100/F/004. Washington, DC: EPA.
- EPA. 2016b. EJ 2020 Action Agenda: The U.S. EPA’s Environmental Justice Strategic Plan for 2016–2020. Washington, DC: EPA.
- Epanchin-Niell, R.S., J.W. Boyd, M.K. Macauley, L. Scarlett, C.D. Shapiro, and B.K. Williams. 2018. Integrating Adaptive Management and Ecosystem Services Concepts to Improve Natural Resource Management: Challenges and Opportunities. Reston, VA: U.S. Geological Survey.
- FAO (Food and Agriculture Organization). 2010. Global Forest Resources Assessment 2010. Rome: FAO.
- Fisher, B., and R.K. Turner. 2008. Ecosystem service: Classification for valuation. *Biological Conservation* 141(5):1167–1169.
- Flory, S.L., K.A. Lorenz, D.R. Gordon, and L.E. Sollenberger. 2012. Experimental approaches for evaluating the invasion risk of biofuel crops. *Environmental Research Letters* 7(4):045904.
- Gandhi, K.J., and D.A. Herms. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biological Invasions* 12(2):389–405.
- Gómez-Aparicio, L., C.D. Canham, and P.H. Martin. 2008. Neighbourhood models of the effects of the invasive *Acer platanoides* on tree seedling dynamics: Linking impacts on communities and ecosystems. *Journal of Ecology* 96(1):78–90.
- Gordon, D.R., D.A. Onderdonk, A.M. Fox, and R.K. Stocker. 2008. Consistent accuracy of the Australian weed risk assessment system across varied geographies. *Diversity and Distributions* 14(2):234–242.
- Guston, D.H. 1999. Evaluating the first U.S. consensus conference: The impact of the citizens’ panel on telecommunications and the future of democracy. *Science, Technology and Human Values* 24(4):451–482.
- Häggman, H., A. Raybould, A. Borem, T. Fox, L. Handley, M. Hertzberg, M.Z. Lu, P. Macdonald, T. Oguchi, G. Pasquali, and L. Pearson. 2013. Genetically engineered trees for plantation forests: Key considerations for environmental risk assessment. *Plant Biotechnology Journal* 11(7):785–798.
- Hansen, A.J., R.R. Neilson, V.H. Dale, C.H. Flather, L.R. Iverson, D.J. Currie, S. Shafer, R. Cook, and P.J. Bartlein. 2001. Global change in forests: Responses of species, communities, and biomes. *BioScience* 51(9):765–779.
- Hayes, K.R., H.M. Regan, and M.A. Burgman. 2007. Introduction to the concepts and methods of uncertainty analysis. Pp. 188–208 in *Environmental Risk Assessment of Genetically Modified Organisms. Volume 3. Methodologies for Transgenic Fish in Developing Countries*, A.R. Kapuscinski, K.R. Hayes, S. Li, and G. Dana, eds. Wallingford, UK: CAB International.
- Hoienicka, H., and M. Fladung. 2006. Biosafety in *Populus* spp. and other forest trees: From non-native species to taxa derived from traditional breeding and genetic engineering. *Trees* 20(2):131–144.
- Holling, C.S. 1978. Adaptive Environmental Assessment and Management. Chichester, UK: John Wiley & Sons.
- Ibáñez, I., J.A. Silander, A.M. Wilson, N. LaFleur, N. Tanaka, and I. Tsuyama. 2009. Multivariate forecasts of potential distributions of invasive plant species. *Ecological Applications* 19(2):359–375.

- Ibáñez, I., J.M. Diez, L.P. Miller, J.D. Olden, C.J.B. Sorte, D.M. Blumenthal, B.A. Bradley, C.M. D'Antonio, J.S. Dukes, R.I. Early, E.D. Grosholz, and J.J. Lawler. 2014. Integrated assessment of biological invasions. *Ecological Applications* 24(1):25–37.
- Johnston, R.J. 2018. Forest Health and Biotechnology within an Ecosystem Services Framework. Presentation to National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, February 8, Washington, DC.
- Joss, S. 1998. Danish consensus conferences as a model of participatory technology assessment: An impact study of consensus conferences on Danish parliament and Danish public debate. *Science and Public Policy* 25(1):2–22.
- Keane, R.M., and M.J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17(4):164–70.
- Kinchy, A.J. 2012. *Seeds, Science, and Struggle: The Global Politics of Transgenic Crops*. Cambridge, MA: MIT Press.
- Kinloch, B.B., Jr., D.A. Davis and D. Burton. 2008. Resistance and virulence interactions between two white pine species and blister rust in a 30-year field trial. *Tree Genetics & Genomes* 4(1):65–74.
- Kleinman, D.L., J.A. Delborne, and A.A. Anderson. 2011. Engaging citizens: The high cost of citizen participation in high technology. *Public Understanding of Science* 20(2):221–240.
- Kleinman, D.L., M. Powell, J. Grice, J. Adrian, and C. Lobes. 2007. A toolkit for democratizing science and technology policy: The practical mechanics of organizing a consensus conference. *Bulletin of Science, Technology & Society* 27(2):154–169.
- Koop, A.L., L. Fowler, L.P. Newton, and B.P. Caton. 2012. Development and validation of a weed screening tool for the United States. *Biological Invasions* 14(2):273–294.
- Kowarik, I. 1995. Time lags in biological invasions with regard to the success and failure of alien species. Pages 15–38 in *Plant Invasions—General Aspects and Special Problems*, P. Pysek, M. Rejmanek, and M. Wade, eds. Amsterdam: SPB Academic.
- Kremen, C. 2005. Managing ecosystems services: What do we need to know about their ecology? *Ecology Letters* 8(5):468–479.
- Kuparinen, A., and F.M. Schurr. 2007. Assessing the risk of gene flow from genetically modified trees carrying mitigation transgenes. *Biological Invasions* 10(3):281–290.
- LaFleur, N., C. Merow, M. Rubega, and J. Silander. 2009. Predicting the rate of spread for a bird-dispersed invasive plant using simulation modeling. *Integrative and Comparative Biology* 49:E96.
- Linacre, N.A., and P.K. Ades. 2004. Estimating isolation distances for genetically modified trees in plantation forestry. *Ecological Modeling* 179(3):247–257.
- Lorentz, K.A., and P.J. Minogue. 2015. Exotic Eucalyptus plantations in the southeastern US: Risk assessment, management and policy approaches. *Biological Invasions* 17(6):1581–1593.
- Lovett, G.M., M. Weiss, A.M. Liebhold, T.P. Holmes, B. Leung, K.F. Lambert, D.A. Orwig, F.T. Campbell, J. Rosenthal, D.G. McCullough, R. Wildova, M.P. Ayres, C.D. Canham, D.R. Foster, S.L. LaDeau, and T. Weldy. 2016. Nonnative forest insects and pathogens in the United States: Impacts and policy options. *Ecological Applications* 26(5):1437–1455.
- Luo, Y., K. Ogle, C. Tucker, S. Fei, C. Gao, S. LaDeau, J.S. Clark, and D.S. Schimel. 2011. Ecological forecasting and data assimilation in a data-rich era. *Ecological Applications* 21(5):1429–1442.
- Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10(3):689–710.
- Mantyniemi, S., L. Uusitalo, H. Peltonen, P. Haapasaari, and S. Kuikka. 2013. Integrated, age-structured, length-based stock assessment model with uncertain process variances, structural uncertainty, and environmental covariates: Case of Central Baltic herring. *Canadian Journal of Fisheries and Aquatic Sciences* 70(9):1317–1326.
- Marco, D.E., M.A. Montemurro, and S.A. Cannas. 2011. Comparing short and long-distance dispersal: modelling and field case studies. *Ecography* 34(4):671–682.
- Maron, J.L., and M. Vilà. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95(3):361–373.
- McDougall, K.L., A.A. Khuroo, L.L. Loope, C.G. Parks, A. Pauchard, Z.A. Reshi, I. Rushworth, and C. Kueffer. 2011. Plant invasions in mountains: Global lessons for better management. *Mountain Research and Development* 31(4):380–387.
- MEA (Millennium Ecosystem Assessment). 2005. *Ecosystems and Human Well-Being: Synthesis*. Washington, DC: Island Press.

- Mellert, K.H., V. Deffner, H. Kuchenhoff, and C. Kolling. 2015. Modeling sensitivity to climate change and estimating the uncertainty of its impact: A probabilistic concept for risk assessment in forestry. *Ecological Modelling* 316:211–216.
- Meirmans, P.G., J. Bousquet, and N. Isabel. 2009. A metapopulation model for the introgression from genetically modified plants into their wild relatives. *Evolutionary Applications* 2(2):160–171.
- Millar, C.I., N.L. Stephenson, and S.L. Stephens. 2007. Climate change and forests of the future: Managing in the face of uncertainty. *Ecological Applications* 17(8):2145–2151.
- Morin, X., and W. Thuiller. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90(5):1301–1313.
- Munns, W.R. Jr., A.W. Rea, G.W. Suter, L. Martin, L. Blake-Hedges, T. Crik, C. Davis, G. Ferreira, S. Jordan, M. Mahoney, and M.G. Barron. 2016. Ecosystem services as assessment endpoints for ecological assessment. *Integrated Environmental Assessment and Management* 12(3):522–528.
- NASEM (National Academies of Sciences, Engineering, and Medicine). 2016. *Genetically Engineered Crops: Experiences and Prospects*. Washington, DC: The National Academies Press.
- NASEM. 2017. *Preparing for Future Products of Biotechnology*. Washington, DC: The National Academies Press.
- Nathan, R. 2006. Long-distance dispersal plants. *Science* 313(5788):786–788.
- National Ecosystem Services Partnership. 2018. *Federal Resource Management and Ecosystem Services Online Guidebook*. Available at www.nespguidebook.com. Accessed July 14, 2018.
- Nijnik, M., and D. Miller. 2017. Valuation of ecosystem services: Paradox or Pandora’s box for decision-makers? *One Ecosystem* 2:e14808.
- NRC (National Research Council). 1996. *Understanding Risk: Informing Decisions in a Democratic Society*. Washington, DC: National Academy Press.
- NRC. 2005. *Valuing Ecosystem Services: Toward Better Environmental Decision-making*. Washington, DC: The National Academies Press.
- Olander, L., R.J. Johnston, H. Tallis, J. Kagan, L. Maguire, S. Polasky, D. Urban, J. Boyd, L. Wainger, and M. Palmer. 2015. *Best Practices for Integrating Ecosystem Services into Federal Decision Making*. Durham: National Ecosystem Services Partnership, Duke University.
- Paillet, F.L. 2002. Chestnut: History and ecology of a transformed species. *Journal of Biogeography* 29(10–11):1517–1530.
- Pearce, D., G. Atkinson, and S. Mourato. 2006. *Cost Benefit Analysis and the Environment: Recent Developments*. Paris: OECD.
- Pheloung, P.C., P.A. Williams, and S.R. Halloy. 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management* 57(4):239–251.
- Poland, T.M., M.R. Emery, T. Ciaramitaro, E. Pigeon, and A. Pigeon. 2017. Emerald ash borer, black ash, and Native American basketmaking; Invasive insects, forest ecosystems and cultural practices. Pp. 127–140 in *Biodiversity, Conservation, and Environmental Management in the Great Lakes Basin*, E. Freedman and M. Meuzil, eds. Abingdon, UK: Routledge.
- Rask, M. and R. Worthington. 2015. *Governing Biodiversity through Democratic Deliberation*. New York: Routledge.
- Rask, M., R. Worthington, and M. Lammi, eds. 2012. *Citizen Participation in Global Environmental Governance*. London: Earthscan Publications.
- Reinhart, K.O., A. Packer, W.H. van der Putten, and K. Clay. 2003. Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. *Ecology Letters* 6(12):1046–1050.
- Rinella, M.J., and E.C. Luschei. 2007. Hierarchical Bayesian methods estimate invasive weed impacts at pertinent spatial scales. *Biological Invasions* 9(5):545–558.
- Robledo-Arnuncio, J.J., E.K. Klein, H.C. Muller-Landau, and L. Santamaría. 2014. Space, time and complexity in plant dispersal ecology. *Movement Ecology* 2(1):16.
- Rogers, B.M., P. Jantz, and S.J. Goetz. 2017. Vulnerability of eastern US tree species to climate change. *Global Change Biology* 23(8):3302–3320.
- Rowe, G., and L.J. Frewer. 2005. A typology of public engagement mechanisms. *Science, Technology and Human Values* 30(2):251–290.
- Savolainen, O., T. Pyhäjärvi, and T. Knürr. 2007. Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution, and Systematics* 38:595–619.
- Schneider, J., and J. Delborne. 2012. Seeking the spotlight: World wide views and the U.S. media context. Pp. 241–260 in *Citizen Participation in Global Environmental Governance*, M. Rask, R. Worthington, and M. Lammi, eds. London: Earthscan.
- Sclove, R. 2010a. Why the polls on climate change are wrong, March 18. Available at https://www.huffingtonpost.com/richard-sclove-phd/why-the-polls-on-climate_b_331896.html. Accessed December 4, 2018.

- Sclove, R. 2010b. Reinventing technology assessment. *Issues in Science and Technology* 27(1):34–38.
- Scorza, R., A.B. Kriss, A.M. Callahan, K. Webb, M. Demuth, and T. Gottwald. 2013. Spatial and temporal assessment of pollen- and seed-mediated gene flow from genetically engineered plum *Prunus domestica*. *PLoS ONE* 8(10):e75291.
- Shvidenko, A., C.V. Barber, and R. Persson. 2005. Forest and woodland systems. Pp. 587–621 in *Ecosystems and Human Well-being: Current State and Trends, Vol 1*, R. Hassan, R. Scholes, and N. Ash, eds. Washington, DC: Island Press.
- Simberloff, D. 2011. How common are invasion-induced ecosystem impacts? *Biological Invasions* 13(5):1255–1268.
- Slavov, G.T., S. Leonardi, J. Burczyk, W.T. Adams, S.H. Strauss, and S.P. DiFazio. 2009. Extensive pollen flow in two ecologically contrasting populations of *Populus trichocarpa*. *Molecular Ecology* 18(2):357–373.
- Snieszko, R.A., R. Danchok, J. Hamlin, A. Kegley, S. Long, and J. Mayo. 2012. White pine blist rust resistance of 12 western white pine families at three field sites in the Pacific Northwest. Pp. 356–367 in *Proceedings of the Fourth International Workshop on the Genetics of Host–Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees*, R.A. Snieszko, A.D. Yanchuk, J.T. Kliejunas, K.M. Palmieri, J.M. Alexander, and S.J. Frankel, tech. cords. Albany, CA: USDA–FS.
- Snow, A.A. 2002. Transgenic crops—why gene flow matters. *Nature Biotechnology* 20(6):542.
- Strauss, S.H., A. Costanza, and A. Séguin. 2015. Genetically engineered trees: Paralysis from good intentions. *Science* 349(6250):794–795.
- Strauss, S.H., D.L. Kershen, J.H. Bouton, T.P. Redick, H. Tan, and R.A. Sedjo. 2010. Far-reaching deleterious impacts of regulations on research and environmental studies of recombinant DNA-modified perennial biofuel crops in the United States. *BioScience* 60(9):729–741.
- Suter, G.W., II. 2000. Generic assessment endpoints are needed for ecological risk assessments. *Risk Analysis* 20(2):173–178.
- Tsatsakis, A.M., M.A. Nawaz, D. Kouretas, G. Balias, K. Savolainen, V.A. Tutelyan, K.S. Golokhvast, J.D. Lee, S.H. Yang, and G. Chung. 2017. Environmental impacts of genetically modified plants: A review. *Environmental Research* 156:818–833.
- USDA-FS (U.S. Department of Agriculture U.S. Forest Service). National Environmental Policy Act Procedures. *Federal Register* 73(143):43084–43099.
- USDA-FS. 2012. Mountain Pine Beetle Response Project: Record of Decision. Available at https://www.fs.usda.gov/nfs/11558/www/nepa/81228_FSPLT2_291923.pdf. Accessed November 24, 2018.
- USDA-FS. 2018. Mountain Pine Beetle Response Project Monitoring Report FY 2016 and 2017. Available at https://www.fs.usda.gov/nfs/11558/www/nepa/81228_FSPLT3_4273675.pdf. Accessed November 24, 2018.
- Uusitalo, L., A. Lehtikoinen, I. Helle, and K. Myrberg. 2015. An overview of methods to evaluate uncertainty of deterministic models in decision support. *Environmental Modelling & Software* 63:24–31.
- Vancly, F. 2003. International principles for social impact assessment. *Impact Assessment and Project Appraisal* 21(1):5–12.
- Vaske, J.J. 2008. *Survey Research and Analysis: Applications in Parks, Recreation and Human Dimensions*. State College, PA: Venture.
- Vose, J.M., C.F. Miniati, G. Sun, and P.V. Caldwell. 2015. Potential implications for expansion of freeze-tolerant eucalyptus plantations on water resources in the southern United States. *Forest Science* 61(3):509–521.
- Walters, C.J., and R. Hilborn. 1978. Ecological optimization and adaptive management. *Annual Review of Ecology and Systematics* 9(1):157–188.
- Wikle, C.K. 2015. Hierarchical models for uncertainty quantification: An overview. In *Handbook of Uncertainty Quantification*, R. Ghanem, D. Higdon, and D. Owhadi, eds. Switzerland: Springer International.
- Williams, B.K. 2011. Passive and active adaptive management: Approaches and an example. *Journal of Environmental Management* 92(5):1371–1378.
- Williams, C.G. 2010. Long-distance pine pollen still germinates after meso-scale dispersal. *Reproductive Biology* 97(5):846–855.

Current Regulatory System for Biotech Trees and Other Methods Used to Address Forest Health

Consistent with the statement of task for this report, this chapter sets forth the U.S. federal regulatory system for any biotech trees as of 2018, including biotech trees developed to address forest health problems. It then analyzes whether that regulatory system, as currently constituted, evaluates the issues that are encompassed by this report's definition of forest health and ecosystem service components when making regulatory decisions on those biotech trees. The chapter also sets forth the federal regulatory system for other human interventions that attempt to address forest health that are not a biotech tree (e.g., pesticides and biocontrol agents) and whether those regulatory systems make approval decisions that take into account the broad range of issues in this report's definition of forest health.

Biotech trees developed to address forest health are regulated under the same statutes and regulations as any biotech plant, including commercial biotech trees (such as the virus-resistant papaya, nonbrowning apple, or cold-tolerant eucalyptus). That regulatory system was established in 1986 when the White House's Office of Science and Technology Policy published the "Coordinated Framework for the Regulation of Biotechnology" (Coordinated Framework), which is not a statute or regulation but a federal policy statement that established principles on how the federal government regulates biotechnology products. The Coordinated Framework stated that different agencies in the federal government should apply existing statutes to biotechnology products (OSTP, 1986).¹ The Coordinated Framework was partially updated in 1992 to provide further policy guidance to federal agencies and more comprehensively updated in 2017 to provide further clarity and transparency to the public and interested stakeholders (EOP, 2017).² Under the Coordinated Framework, as many as three different federal agencies—the U.S. Department of Agriculture (USDA), the U.S. Environmental Protection Agency (EPA), and the U.S. Food and Drug Administration (FDA)—could regulate a biotech tree developed to address forest health.

It is important to note that biotechnological approaches have advanced since the Coordinated Framework was established as is acknowledged in the "National Strategy for Modernizing the Regulatory System for Biotechnology Products" (EOP, 2016), which the White House released in September 2016. The National Strategy mentioned that the federal government would provide additional guidance on how it will regulate products produced through new biotechnologies such as genome editing³ because the different federal statutes grant each agency authority to regulate specific products, not the process by which they are

¹The Coordinated Framework presents information about the agencies' roles and responsibilities in several forms such as graphics that illustrate agency-specific roles and a table summarizing the responsibilities for different product categories.

²A detailed discussion of the history of the Coordinated Framework and the policies it established can be found in the National Academies reports *Genetically Engineered Crops: Experiences and Prospects* (NASEM, 2016) and *Preparing for Future Products of Biotechnology* (NASEM, 2017). The controlling document is the 2017 version of the Coordinated Framework.

³The National Strategy set forth a commitment by USDA, EPA, and FDA to clarify oversight of new biotechnology products, such as products produced using genome editing and genetically engineered insects.

produced. The application of the Coordinated Framework to specific products means that biotech trees and plants may be regulated by zero, one, two, or three or more agencies.⁴

U.S. DEPARTMENT OF AGRICULTURE

USDA is the first or primary agency that regulates some biotech plants. It regulates the import, interstate movement, transport, and environmental release of biotech plants that fall under the *Code of Federal Regulations* (CFR), specifically found at 7 CFR Part 340 and issued under the Plant Protection Act as amended December 23, 2004, 7 U.S.C. § 7701 et seq.⁵ Those regulations ensure that these plants are not “plant pests,” which are defined as “any living stage of a pest that can directly or indirectly injure, cause damage to, or cause disease in any plant or plant product” (7 CFR § 340.1). Biotech plants could become a plant pest if they carry the genes or DNA of species that have been determined to cause injury to other plants (e.g., when *Agrobacterium*-mediated transformation is used to introduce desired genes; Gelvin, 2003). USDA interprets that legal authority so that a biotech plant or tree is regulated if

1. the biotech plant or tree has pests that are on USDA’s list of plant pests,
2. the process of introducing the change in the plant or tree’s genome involves an organism on the list of plant pests (such as *Agrobacterium* mediated transformation), or
3. any of the introduced DNA (the gene, promotor, terminator, etc.) came from an organism on the list of plant pests (7 CFR § 340.1).

Under those regulations, any regulated biotech plants must be submitted to one of three oversight processes before that plant can be released into the environment. The first process, known as “notification,” is used for limited field trials of a biotech plant that meets certain eligibility criteria and field trial containment standards. The applicant provides USDA with a notification detailing the release, and USDA has 30 days to respond (USDA-APHIS, 2011). As many as 1,000 field trials, mostly for grains, fruits, and vegetables are authorized each year using this procedure. In 2008, USDA determined “based upon accumulated regulatory experience and currently available science” that it would no longer accept notifications for environmental releases lasting more than 1 year (USDA-APHIS, 2008). Thus, no biotech tree that falls under USDA’s jurisdiction can qualify for the notification process since it is virtually impossible to complete a field trial with a tree in less than 365 days.

The second process to get permission for a limited release of a biotech plant is the USDA “permitting” process. That process requires a more detailed application and a longer review time at USDA before the release is authorized (USDA, 2017e). Permitting is not as common as the notification, although USDA has issued hundreds of permits since it began regulating biotech crops (USDA, 2017b). Since 2008, all experiments with biotech trees that are regulated under 7 CFR Part 340, independent of whether those trees are developed to address forest health, require a permit before any release into the environment (USDA-APHIS, 2008).

The third process is called a “petition for non-regulated status,” where a developer requests that USDA determine that there is no plant pest risk from the biotech plant, and it is no longer regulated (USDA-APHIS, 2016). The petition process is the primary path to commercialization, and more than 124 crops

⁴The Coordinated Framework identifies agencies other than USDA, EPA, and FDA that would regulate different products of biotechnology. More discussion about other agencies can be found in Chapter 3 of the National Academies’ report *Preparing for Future Products of Biotechnology* (NASEM, 2017).

⁵Available at https://www.aphis.usda.gov/plant_health/downloads/plant-protect-act.pdf. Accessed July 19, 2018. USDA has twice proposed revisions to 7 CFR Part 340, once in 2008 and again in 2017; both proposals were later withdrawn. Until 7 CFR Part 340 is changed, the regulatory system described in this chapter is what will be applied to trees developed with biotechnology.

have been deregulated. As of 2018, three biotech fruit trees—transgenic papaya and plum⁶ and apple transformed via RNA interference—have successfully been granted nonregulated status, but no biotech plantation trees or trees with traits to address forest health had been granted that status. As the time the committee was writing its report, one petition for a eucalyptus tree (*Eucalyptus urograndis*) is pending but that tree is not being developed to address forest health (USDA-APHIS, 2018b).

To decide whether to grant a petition for nonregulated status, USDA’s regulatory review is limited to determining whether the biotech plant poses a “plant pest” risk. The risk assessment process (NASEM, 2016:475)

considers, among other things, whether the [genetically engineered (GE)] crop is more likely than its non-GE comparator to become invasive or weedy, to be more susceptible to pests or diseases, or to have greater effects on nontarget organisms. [USDA’s Animal and Plant Health Inspection Service (APHIS)] also considers the potential effects of gene flow to wild relatives and other organisms. In effect, APHIS uses the risk-assessment process to determine whether a GE crop is likely to pose a greater “plant pest” risk than a comparable conventionally bred crop variety.

According to USDA, that review process culminates in a document, the Plant Pest Risk Assessment, which is the primary document used to determine whether to grant the petition. That document is not specifically required to address broad forest health concerns, only plant pest concerns. However, if forest health would be impacted because the biotech tree might have a plant pest concern, such as it could become invasive or have an impact on nontarget organisms, then those issues would be assessed in the Plant Pest Risk Assessment.

In addition to addressing any plant pest issues with a biotech plant, any decisions by USDA to issue a permit for a field trial or to grant a petition for nonregulated status also must comply with the National Environmental Policy Act, 42 U.S.C. § 4321 et seq. (NEPA).⁷ NEPA was established so that the government and the public would be aware of the environmental impact of government actions. Thus, NEPA requires federal agencies to assess the environmental impact of all major federal actions and make that assessment public. That analysis covers the effects on the “human environment,” which is interpreted comprehensively to include the natural and physical environment and the relationship of people to that environment (42 U.S.C. § 4332(C)). Effects (and impacts) include:

ecological (such as the effects on natural resources and on the components, structures, and functioning of affected ecosystems), aesthetic, historic, cultural, economic, social, or health, whether direct, indirect, or cumulative. Effects may also include those resulting from actions which may have both beneficial and detrimental effects, even if on balance the agency believes that the effect will be beneficial. (40 CFR § 1508.8⁸)

For each permit or grant of nonregulated status by USDA, compliance with NEPA can consist of conducting an environmental assessment (EA) and a finding of no significant impact (FONSI). However, if the agency cannot make a FONSI determination after the completion of the EA, it must conduct a more detailed and time-consuming environmental impact statement (EIS) and a record of decision (ROD). Although agencies must go through the NEPA assessment process, NEPA does not give agencies any authority to make substantive decisions based on the results of their environmental assessment. In other words, NEPA requires an assessment of impacts but does not provide any basis for denying or modifying a government action

⁶Plum resistant to plum pox virus has been deregulated but had not been planted commercially in the United States as of 2018.

⁷Available at <https://www.gpo.gov/fdsys/pkg/CFR-2017-title40-vol37/xml/CFR-2017-title40-vol37-sec1508-8.xml>. Accessed July 19, 2018.

⁸Available at <https://www.gpo.gov/fdsys/pkg/CFR-2017-title40-vol37/xml/CFR-2017-title40-vol37-sec1508-8.xml>. Accessed July 19, 2018.

based on that assessment. The EA or EIS provides information about impacts but does not change the government agency's proposed action unless the statute under which the agency is carrying out its activity or action itself allows the agency to take into account the environmental analysis in making its decision.

USDA has received more than 21,000 requests under either the notification or permitting process to grant a permit to conduct a field trial with a biotech organism that could be a potential plant pest. Of that amount, there have been approximately 1,329 notifications received by USDA for such trees and 1,191 have been acknowledged and allowed to proceed (see Figure 6-1). USDA has also received approximately 441 permit applications for biotech trees and issued 387 permits (Figure 6-2). It has issued 220 permits to biotech nonfruit tree species and 167 permits for biotech fruit trees (USDA-APHIS, 2018a). For the permits issued for biotech trees, only 17 of them required an EA under NEPA, 5 fruit tree applications and 12 nonfruit tree applications (see Figure 6-3). Therefore, USDA completed an EA and FONSI for approximately 4 percent of its permit decisions for biotech trees. It should be noted that no field trial with a biotech forest tree (such as the transgenic chestnut) has required an EA for a field trial. All 12 EAs for nonfruit trees involved commercial plantation species (USDA-APHIS, 2017c).

As of May 2018, USDA had processed 124 petitions for nonregulated status for biotech plants that could pose a plant pest risk. To make decisions on those petitions and comply with NEPA, USDA generated 110 EAs with a FONSI and nine EISs (only five petitions had a FONSI). Six of the 124 petitions involved tree species—five for fruit trees and one for eucalyptus—and USDA carried out four EAs for the fruit trees (only one petition received a FONSI) and an EIS for the eucalyptus. Therefore, USDA carries out an EIS for a small minority of the petitions it receives, although the one nonfruit tree petition did require an EIS (USDA-APHIS, 2018b).

To the extent that USDA is going to assess forest health issues involving biotech trees, it is likely to occur in its compliance with NEPA. USDA has not completed an EIS for a native biotech forest tree, but it did complete an EIS for a frost-tolerant eucalyptus tree (see Box 6-1) (USDA-APHIS, 2017a). Although for a commercial plantation tree, that EIS can provide some insight into what an EIS for a biotech tree developed for addressing forest health might cover.

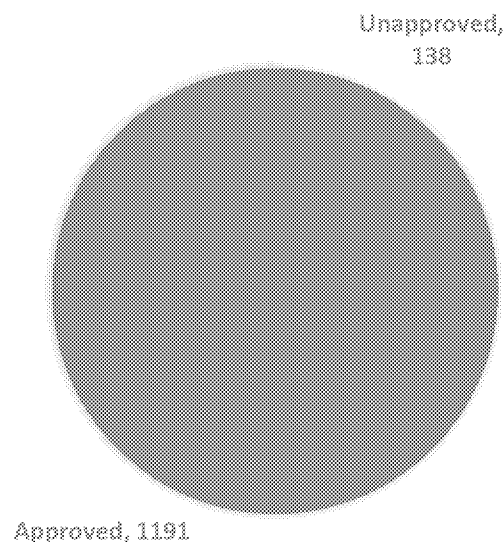


FIGURE 6-1 Approved and unapproved notifications for biotech trees submitted to the U.S. Department of Agriculture for field trials. SOURCE: Data from USDA-APHIS, 2018a.

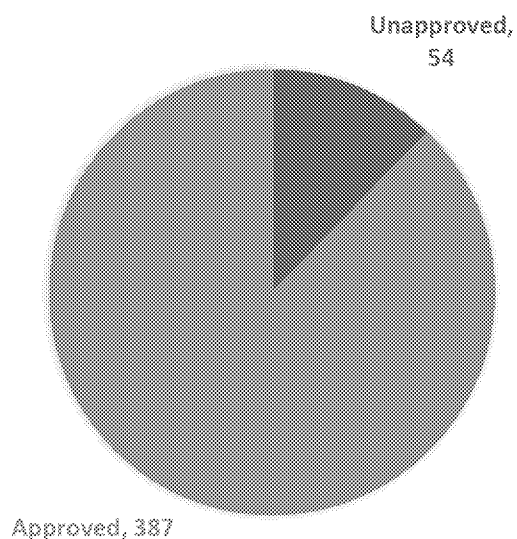


FIGURE 6-2 Approved and unapproved permits for biotech trees submitted to the U.S. Department of Agriculture. SOURCE: Data from USDA-APHIS, 2018a.

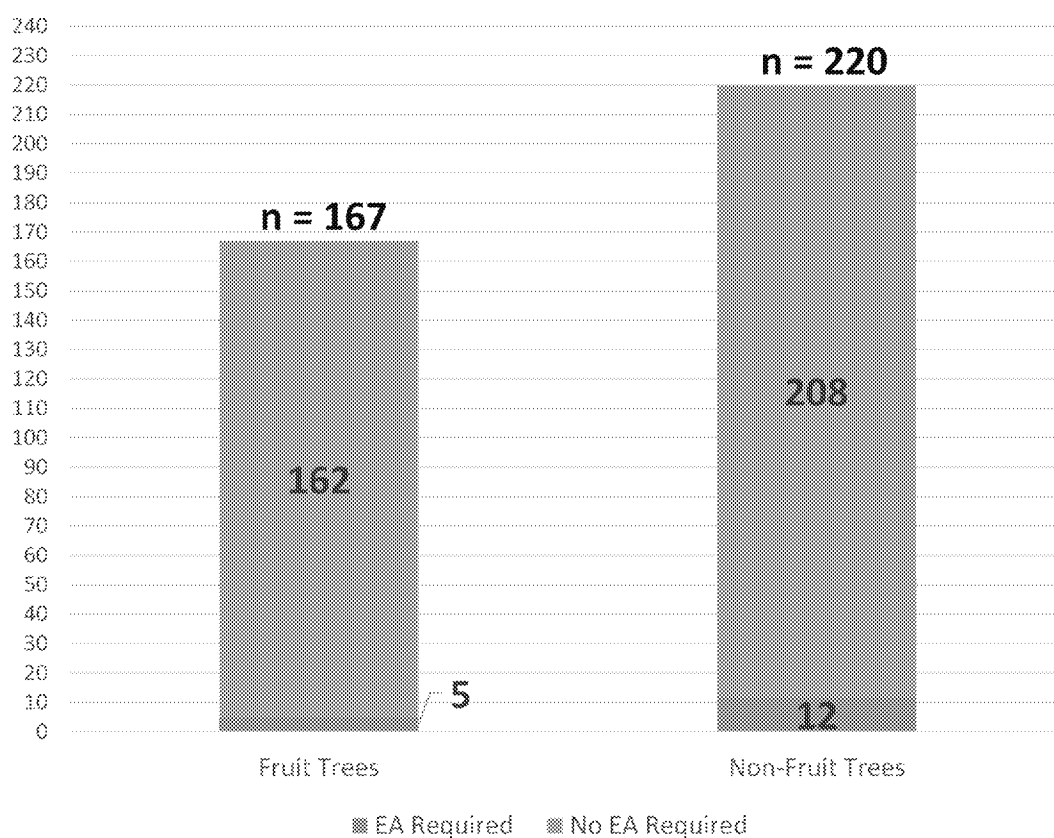


FIGURE 6-3 Permits issued for biotech trees requiring an environmental assessment (EA). SOURCE: Data from USDA-APHIS, 2018a).

BOX 6-1 How the U.S. Department of Agriculture Environmental Impact Statement for Transgenic Frost-Tolerant Eucalyptus Trees Addresses Forest Health

USDA stated that it prepared an EIS for transgenic eucalyptus (*Eucalyptus urograndis*) because:

[t]he cultivation of freeze tolerant eucalyptus (FTE) may potentially impact a wide scope of environmental values, including alteration in susceptibility of FTE to disease or insects, alteration in weediness characteristics, potential impacts on soil hydrology and water resources, potential impacts on fire incidence, ecology, forestry practices or land use, and potential direct or indirect effects on human health, wildlife, and their habitats. Preparation of an EIS will enable APHIS to evaluate these and other issues related to the Agency's decision-making regarding the petition for nonregulated status. (USDA-APHIS, 2013)

Overall, the FTE EIS completed by USDA assesses some components of “forest health” that are regulating and supporting services. For example, it looks at impacts on land use if FTE are available for planting and what types of trees it will replace (primarily pine). The EIS determines that the FTE will not impact air quality but will have local and direct impacts on water quantity and quality because FTE will use more water than other types of vegetation and increase sediment loading from forest systems into forest streams. The EIS analyzed the potential impacts on wildlife, finding that planting of FTEs will reduce the available understory vegetation for wildlife, provide less food for small mammals and deer, and reduce the number of bird species (due to reduced, less nutritious, smaller seeds, and less habitat for shelter and nesting). It analyzed whether the planting of FTEs would increase insect and disease pests associated with eucalyptus and whether it would expand the area where those pests are found. Finally, it concluded that “biological diversity is likely to be reduced when compared to planted pine plantations within the action area, primarily due to the impacts from short-rotation management of FTE on vegetation and subsequent impacts on wildlife” (USDA-APHIS, 2017a). Thus, it is fair to say that if USDA conducts an EIS under NEPA for a biotech tree developed for forest health, it would likely assess a number of environmental and ecological parameters and services that would fall within this committee's definition of forest health.

The USDA EIS for FTE generally does not analyze many of the ecosystem services that are classified as provisioning and cultural services. There is no discussion about the effects of planting FTE trees on recreation uses or tourism, nor anything about other potential values that humans might attach to the forest areas where the trees will be planted (USDA-APHIS, 2017a). However, USDA is required to comply with several laws and Executive Orders, which can be considered policies that require some limited and indirect analysis of some provisional and cultural ecosystem services. For example, USDA is required to conduct an analysis of impacts of its decision on endangered and threatened species under the Endangered Species Act of 1973 and to analyze impacts on migratory birds under an Executive Order to protect migratory birds—policies that could be interpreted to capture aspects of provisioning and cultural services (Clinton, 2001). The EIS found that planting FTE trees could affect the critical habitat of many listed species (USDA-APHIS, 2017a). Also, a NEPA EIS must comply with the Executive Orders 12898, Environmental Justice in Minority and Low-Income Populations (Clinton, 1994), 13045, Protection of Children from Environmental Health Risks and Safety Risks (Clinton, 1997), and 13175, Consultation and Coordination with Indian Tribal Government (Clinton, 2000). Complying with each of those Executive Orders requires at least a limited analysis of issues that could be considered in some cases as provisional or cultural services pertaining to forest health, but it is unlikely to ever include analysis of cultural or spiritual elements from a healthy forest. Therefore, to the extent that a particular ecosystem service can be captured by one of several overarching federal laws and policies, it is likely to be analyzed in the NEPA EIS process. If it cannot be captured under those specific laws and policies, it will likely be absent from any analysis and decision making, depending upon the particular ecosystem service at issue.

Not all biotech plants or trees are regulated under 7 CFR Part 340, which only applies to potential “plant pests.” Since around 2010, USDA has utilized its “Am I regulated” procedure to identify approximately 68 biotech plants that do not involve plant pests and need not comply with 7 CFR Part 340. That

includes biotech plants developed using biolistics as well as many plants whose genomes were altered with genome-editing techniques such as zinc finger nucleases, transcription activator-like effector nucleases, and the clustered regularly interspaced short palindromic repeat (CRISPR)-Cas9 nuclease system. It also includes genome-edited plants that use *Agrobacterium* to introduce the genome-editing cassette as long as the final product contains no introduced genetic material. At the time the committee was writing its report, countries around the world were in the process of determining how agricultural products produced using genome-editing techniques would be regulated, if at all. The European Court of Justice ruled in July 2018 that those products would be considered “GMOs” under the European Union’s GMO Directive 2001/18 and would not qualify for an exemption from the substantive requirements of that Directive as is the case for products produced with chemical mutagenesis or irradiation. Thus, this decision means that genome-edited agricultural products will be regulated very differently in the European Union than how many genome-edited crops are regulated at USDA, which could have significant trade implications.⁹ As of August 2018, USDA has received one “Am I regulated” request for a biotech tree, a loblolly pine, and found that it did not fall within USDA’s oversight because the added genetic material did not involve any plant pest and the transfer of genetic material was achieved by biolistics (USDA-APHIS, 2018c). Unless the regulations in 7 CFR Part 340 are revised, it is safe to assume that there will be future biotech trees, including trees developed to address forest health, that will not be required to obtain a permit or the granting of nonregulated status before that tree is released into the environment.

In conclusion, not all biotech trees developed to address forest health will be regulated by USDA under its authority through the Plant Protection Act’s 7 CFR Part 340. If a biotech tree falls within USDA’s legal mandate involving “plant pests,” then it will require a permit for field trials and cannot qualify for the quicker “notification” process. It will also need to petition for nonregulated status where the agency will conduct a Plant Pest Risk Assessment and comply with NEPA. USDA’s review of any application under its plant pest authority might include some aspects of forest health. That review would be due to the unique biological characteristics of trees and not because USDA specifically considers forest health issues in its Plant Protection Act decision process. USDA only considers forest health issues in the Plant Pest Risk Assessment if those issues are also “plant pest” issues, such as weediness or impacts on nontarget organisms. USDA may consider some forest health issues in its compliance with NEPA, but that analysis is much more likely when USDA conducts an EIS and not the less burdensome EA. However, USDA has only conducted an EIS on a few of the petitions it has granted and only one on a biotech tree (out of six applications). Similarly, USDA only conducts an EA for a small number of permit applications and has only conducted such an EA on approximately 4 percent of the biotech trees it has permitted. Therefore, since the primary way that USDA’s oversight under the Plant Protection Act considers forest health issues is through compliance with NEPA, and the historical rate of conducting an EIS and EA for a biotech tree is very low, then without substantial revision to regulatory statutes, guidelines, or practice, most biotech trees will not be comprehensively evaluated for their impacts on forest health, as defined in this report. In addition, the NEPA process is procedural, so it does not provide USDA with any authority to address forest health impacts that are identified in an EA or EIS.

U.S. ENVIRONMENTAL PROTECTION AGENCY

EPA regulates some biotech plants under the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA, 7 U.S.C. § 135 et seq.) and the Federal Food, Drug and Cosmetic Act.¹⁰ Under FIFRA, EPA regulates the sale, distribution, and use of pesticides through a premarket mandatory registration process, and plants that have a protectant incorporated into them using biotechnology (called “plant incorporated

⁹Judgment of 25 July 2018, *Confédération paysanne and others*, C-528/16, EU:C:2018:583.

¹⁰EPA’s role under the Federal Food, Drug and Cosmetic Act involves determining a tolerance level for any pesticide residues that would remain on human food. This portion of EPA’s mandate has little applicability for biotech forest trees, and so it is not discussed in detail in this chapter.

protectants” or PIPs) are captured under regulations found in 40 CFR Parts 152 and 174. According to those regulations, “a pesticide is a substance or mixture intended to prevent, destroy, repel or mitigate any pest” (40 CFR § 152.3)¹¹ and a PIP “is a pesticidal substance intended to be produced and used in a living plant and the genetic material necessary for its production” (40 CFR § 174.3).¹² For those products, “registration requires an evidence-based premarket review in which product sponsors submit evidence to demonstrate that the product will not cause unreasonable adverse effects on the environment under its proposed conditions of use” (NASEM, 2017:90). The scope of the evaluation of a PIP by EPA is no different than its evaluation of more traditional chemical or biological pesticides. EPA addresses environmental impacts as well as impacts on humans and other species (such as insects and aquatic organisms). As stated in more detail below, that assessment covers some ecological aspects of forest health but misses the less quantitative ecosystem services a healthy forest provides (see section “Regulation of the Use of Conventional Pesticides to Address Forest Health,” below).

If a biotech tree is a PIP under EPA regulations—for example, if a *Bacillus thuringiensis* (*Bt*) gene were added to a poplar to confer protection against some insect pests—then it would be regulated under FIFRA. As of 2018, EPA has reviewed and registered two biotech fruit trees under its PIP process: a honeysweet plum with a plum pox viral coat protein gene and a papaya tree with a papaya ringspot virus coat protein gene (EPA, 2010, 2015, 2017). A review of the EPA decision documents for those two products does not reveal any special environmental considerations or data requirements solely because the protectant is integrated into a tree species instead of a grain or vegetable crop. In fact, the documents supporting those two registration decisions involve less data and a shorter overall assessment than for *Bt* crops. However, those two examples are not necessarily predictive about how EPA would review a protectant in a forest tree. It should also be noted that when EPA registers a pesticide, there is continuing oversight responsibility and the potential that the pesticide’s product registration will need to be renewed after a specified number of years or the use of the product will become illegal. This ongoing responsibility is different from USDA’s oversight because, once the nonregulated petition is granted, USDA has no oversight role going forward. EPA has stated that this continuing oversight could raise specific challenges for forest trees with incorporated protectants because if the PIP’s registration is not renewed, the biotech trees could have migrated throughout the landscape and could not easily be recalled or eliminated.

U.S. FOOD AND DRUG ADMINISTRATION

FDA regulates biotech plants if they produce food for humans or feed for animals. FDA uses its food-safety authority under the Federal Food, Drug and Cosmetic Act (FFDCA, 21 U.S.C. § 301 et seq.) to oversee the safety of all foods, including foods derived from biotech crops. Under this authority, FDA requires mandatory approvals of food additives but determined in a policy statement issued in 1992 that biotech food crops are generally not “food additives” requiring approval. Instead, FDA set up a voluntary consultation process by which biotech crop developers can share food safety data with FDA, and the agency can identify any deficiencies in the developer’s food and feed safety risk assessment (FDA, 1992). As of 2018, approximately 150 biotech crops had completed the FDA voluntary consultation process (FDA, 2018). Products that have completed the voluntary consultation process include biotech apple, plum, and papaya fruit trees but no forest tree species. However, it is anticipated that biotech forest trees that have edible portions, such as the transgenic chestnut, could voluntarily participate in the FDA consultation process (see Box 6-2). The FDA voluntary review process is limited to food and feed safety issues of a biotech plant. They do not address any aspects of this report’s definition of forest health.

¹¹ Available at <https://www.gpo.gov/fdsys/granule/CFR-2012-title40-vol25/CFR-2012-title40-vol25-sec152-3>. Accessed July 20, 2018.

¹² Available at <https://www.gpo.gov/fdsys/granule/CFR-2013-title40-vol25/CFR-2013-title40-vol25-sec174-3>. Accessed July 20, 2018.

BOX 6-2 The Possible Regulatory Pathway for a Transgenic American Chestnut

Of the different case study species in this report, the American chestnut is the furthest along in development and testing and so best illustrates the potential regulatory pathway for a biotech tree developed to address forest health. As discussed in Chapter 3, chestnut trees have been transformed with *Agrobacterium* with an oxalate oxidase (OxO) gene from wheat. The research and development of those transgenic chestnut trees have been regulated by USDA under the Plant Protection Act because the OxO gene was introduced via *Agrobacterium*. USDA has issued 18 permits for the interstate movement/release of a transgenic chestnut tree between 2010 and 2018 to five different institutions (State University of New York, Virginia Polytechnic Institute and State University, The American Chestnut Foundation, University of Georgia, and Biofuels Center of North Carolina) and denied one application (three were also withdrawn). The issuance of those permits did not require USDA to conduct either an EA or an EIS. It is expected that under the current USDA regulations (7 CFR Part 340), if any transgenic chestnut tree is to be released unconfined to propagate naturally in the environment, the developer will be required to submit to USDA a petition for nonregulated status. At that time, USDA will determine whether the proposed action requires only an EA and a finding of no significant impact or an EIS. However, some recent “Am I regulated?” responses from USDA suggest that if there is no DNA from the *Agrobacterium* transformation in the transgenic tree, there may be no need to obtain permits or nonregulated status to release the organism into the environment. If USDA decided that the transgenic chestnut no longer falls within 7 CFR Part 340, then no safety assessment or any NEPA analysis, which would address aspects of ecosystem services, would be required by that agency.

A transgenic American chestnut tree also might fall within the regulatory purview of EPA and FDA. EPA's registration requirements for a pesticide may apply to a biotech chestnut with blight resistance if the introduced trait is acting as a pesticide. This interpretation of EPA's laws and regulations is similar to their actions with the transgenic papaya and transgenic plum trees, which went through the FIFRA registration process. In addition, chestnuts are eaten by humans and fall within the definition of food under the FFDCA. The developers of the biotech chestnut tree could choose to submit to FDA's voluntary consultation process for bioengineered foods, and so FDA could review and provide any comments on the developer's food safety data and analysis. Under the FFDCA, the developer will be responsible for ensuring that the biotech chestnut is as safe as its conventional counterpart.

The discussion of the chestnut in Chapter 3 mentions several other alternatives that are being pursued to address the destruction of the species by chestnut blight. The transferring of resistance from the Chinese chestnut tree through hybridization and selective breeding and the release of those trees into the environment is not subject to regulation by USDA, EPA, or FDA as discussed in this report. Another option for addressing the loss of the American chestnut tree from the chestnut blight fungus is to reduce the ability of the chestnut blight fungus to harm those trees. USDA has issued four release permits to West Virginia University to test chestnut blight fungus that has been genetically engineered to be less damaging to chestnut trees and potentially outcompete the more virulent strain of fungus.

The regulatory pathway for those alternatives to address the loss of the American chestnut tree are significantly different, with some options being highly regulated and others being minimally regulated. For the alternatives, whatever the regulatory oversight, it is clear that the oversight will not consider the range of forest health parameters discussed in this report.

For the other case study species in this report, possible solutions to address the forest health impacts may or may not be regulated depending on what type of solution is pursued, selective breeding or intentional changes to the genome through biotechnology. For products of biotechnology, whether they are regulated and by which agencies will depend on the introduced genetic material and its origin, the way the genetic change was achieved, and the final phenotype of the tree. Determining the regulatory pathway before a product is developed would be speculative. However, for any biotech tree solution, the oversight would be no greater than what is likely for the transgenic American chestnut as that product is regulated by all three possible agencies.

STAKEHOLDER CRITICISM OF FEDERAL OVERSIGHT OF BIOTECH PLANTS AND TREES

There have been many criticisms voiced by different stakeholders about the Coordinated Framework and the oversight performed by USDA, EPA, and FDA. The committee specifically heard from stakeholders about their criticisms of that regulatory system as it applies to biotech trees developed to address forest health (Campbell, 2018; Costanza, 2018; Petermann, 2018; Strauss, 2018). It is outside the scope of this report to analyze the current federal oversight of biotech plants and trees and make observations or recommendations about that oversight. That type of analysis was conducted (not specific to biotech trees) in two recent National Academies studies, and those reports identified recommendations for improving the regulatory system that would impact biotech tree oversight if those recommendations were implemented (NASEM, 2016, 2017).

MOVEMENT OF BIOTECH TREES DEVELOPED TO ADDRESS FOREST HEALTH ACROSS NATIONAL BORDERS

A unique aspect of a biotech tree developed to address forest health is that it will result in an unconfined release into the environment that is meant to propagate, spread, and persist without human oversight and control; this is significantly different from previously developed biotech trees, which are meant to be grown in orchards or plantations, and biotech crops, which are grown on managed farms. Consequently, biotech trees released to address forest health could cross national borders, raising the possibility of a biotech plant being approved for release in one country but not approved in the other country (such as between the United States and Canada). Does the U.S. regulatory system account for this cross-border movement, and how would it deal with the release of a biotech tree that migrated from another country?

When USDA obtains a petition for nonregulated status of a biotech plant, including a biotech tree, it is required to make the petition available to the public and seek comment as well as publicly announce its decision. This process, as well as the Trilateral Technical Working Group of agricultural biotechnology regulators from Canada, Mexico, and the United States would ensure that the neighboring countries are aware of any potential biotech trees that could migrate across borders (Doley, 2018). In addition, while the Plant Pest Risk Assessment need not consider cross-border impacts, USDA's compliance with NEPA also requires that USDA comply with Executive Order 12114 on Environmental Effects Abroad of Major Federal Actions (Carter, 1979).¹³ Therefore, USDA's EA or EIS would need to analyze any environmental effects of migration of the approved biotech tree across the U.S. border, although USDA has no authority to base its decision to grant or deny the petition on that analysis. That analysis, as discussed above, might include some aspects of forest health but likely will not comprehensively cover the topic. Although there are no examples of any analysis required by Executive Order 12114 (Carter, 1979) for biotech plants or trees by USDA, an example of this type of analysis can be found in the NEPA compliance documents for FDA's decision to approve the fast-growing transgenic salmon, which involves production in Canada and Panama (FDA, 2017).

If a biotech tree were introduced in Canada and migrated across the border to the United States and the tree was a product that falls within the regulatory authority of USDA under the Plant Protection Act, then USDA could impose quarantine or other mitigation activities to address the illegally growing biotech trees. USDA could also require the developer to submit a petition for nonregulated status or on its own without any document submitted by the developer conduct a Plant Pest Risk Assessment and environmental analysis under NEPA to determine if the illegal activity should be allowed under the Plant Protection Act. Similar activities by the Canadian regulators might occur if the biotech tree were approved in the United States and migrated to Canada.

¹³See also the National Environmental Policy Act of 1969, as amended. Available at https://www.whitehouse.gov/sites/whitehouse.gov/files/ceq/NEPA_full_text.pdf. Accessed July 19, 2018.

Similar issues could arise in relation to the sovereign boundaries of tribal nations within the United States. For example, Native American Haudenosaunee territories are within the historic range of the American chestnut tree, and the environmental release of a transgenic chestnut might eventually cross their sovereign borders. While consultation processes are formally in place between the U.S. federal government and tribal nations, they have not been uniformly successful in practice, and it is unclear how a difference in policy over a transgenic tree would be negotiated and managed (Barnhill-Dilling, 2018; Patterson, 2018).

The above actions—being aware of cross-border approvals, analyzing environmental impacts, and addressing migrating biotech trees through quarantine or after-the-fact approval—only apply to biotech trees that fall within the mandates of U.S. regulators (and Canadian regulators across the border). As stated earlier in this chapter, some biotech trees may not involve plant pests and fall outside USDA’s legal authority. If that is the case, those trees could be released in the United States without any federal oversight or notice to neighboring countries or tribal nations that they might cross sovereign borders. Similarly, a biotech tree planted in Canada that migrates to the United States might not violate USDA’s biotech regulations under the Plant Protection Act, if it does not involve “plant pests.” However, if it has a PIP incorporated in it, then it might be in violation of EPA’s regulations under FIFRA.

CURRENT REGULATORY SYSTEM FOR OTHER INTERVENTIONS TO ADDRESS FOREST HEALTH

Independent of whether biotech trees are developed and deployed to address forest health issues, there are and will continue to be other methods utilized to address forest health concerns. This includes the use of pesticides, biological control agents, and introduction of tree varieties with resilience characteristics produced through selective-breeding methods. It is helpful to compare how these interventions are regulated before they are adopted to identify differences in the evaluation processes and to determine how the federal regulatory system considers forest health, if at all.

Regulation of the Use of Conventional Pesticides to Address Forest Health

EPA regulates the use of all pesticides, including pesticides used in forests, using three laws: FIFRA, FFDCA, and the Pesticide Registration Improvement Act (7 U.S.C. § 136 et seq.). Any pesticide—which can include conventional pesticides (such as a chemical pesticide) as well as biopesticides (such as a microbial agent)—can obtain a registration from EPA if the agency determines that the pesticide will have no “unreasonable adverse effects on the environment” (FIFRA, 7 U.S.C. § 136(bb)) and there is a “reasonable certainty that no harm [to humans] will result from aggregate exposure [dietary, drinking water and residential exposure] to the pesticide residue” (FFDCA, 21 U.S.C. § 408(c)). Further, FIFRA defines “unreasonable adverse effects on the environment” to mean “any unreasonable risk to man or the environment, taking into account the economic, social and environmental costs and benefits of the use of any pesticide” (7 U.S.C. § 136(bb)).

Before issuing a pesticide registration, EPA conducts a risk assessment, which has a human safety component and an ecological effects component. For conventional, outdoor pesticides that involve a potential food product, this assessment involves a complete suite of tests for pesticide active ingredients, including but not limited to toxicological tests for acute, subchronic, and chronic toxicity, carcinogenicity, neurotoxicity, and immunotoxicity and ecological effects on surrogate species for aquatic, terrestrial, and avian species as well as honeybees (40 CFR Part 158, “Data Requirements for Pesticides”).¹⁴ A similar process occurs for biochemical and microbial pesticides except that, because those products are naturally found in the environment, there is a tiered testing scheme. Under that testing scheme, if no adverse effects are found

¹⁴Pesticides that are designed for use on (or produced in) plants or animals, whose byproducts are not part of the human food supply, generally do not require the carcinogenic and other long-term bioassays listed. Available at <https://www.gpo.gov/fdsys/granule/CFR-2012-title40-vol25/CFR-2012-title40-vol25-part158>. Accessed July 20, 2018.

in lower tiers, there is no need for testing in higher tiers.¹⁵ According to EPA, there are no special regulations or data requirements specific to pesticides used in a forest, and they are assessed under the same procedures and standards as pesticides used in other contexts. However, it is clear that the process for registering any pesticide is extensive and requires addressing several different safety questions with the generation of safety data.

Based on the information provided by EPA, the registration process for pesticides used in forests does not formally take forest health into consideration. However, some portions of their ecological assessment (ecological exposure and toxicity) require data and analysis that address areas that fall within the definition of forest health:

1. The assessment of ecological effects on aquatic, terrestrial, and avian species as well as honeybees;
2. The assessment of environmental fate of the pesticide in various media and its persistence; and
3. Testing and assessing the impacts on nontarget organisms.

EPA is not required to conduct an EIS under NEPA when it registers a pesticide, and so the risk assessment is the only avenue for considering forest health parameters. However, the FIFRA definition of “unreasonable adverse effects on the environment” could allow EPA to integrate social and economic impacts involving forest health into its decision process.

Other agencies, such as USDA’s Forest Service have their own policies and requirements for the use of pesticides for land they manage. According to the Forest Service, pesticides are one component of Integrated Pest Management “to prevent, control, or manage unwanted native plants, animals, and pathogens, and non-native invasive species on all areas of the National Forest System” (USDA–FS, 2013). To use a pesticide on national forest lands, the pesticide use must be reviewed and approved. The form used for the approval asks for standard information when using a pesticide (e.g., pesticide product, application information, treatment area), but no information about potential ecosystem service impacts. The pesticide approval process includes approving the application and complying with NEPA (USDA–FS, 2013).

The Forest Service states that it places “high priority on human and ecological health and safety” and that any use of pesticides “must be based on analysis of effectiveness, specificity, environmental impact, economic efficiency and human exposure” (USDA–FS, 2018a). Thus, the Forest Service conducts a human health and ecological risk assessment (HERA) for commonly used pesticides. According to the Forest Service, “these documents are used to determine the probability of adverse effects to humans, wildlife, and the environment from the use of pesticides” (USDA–FS, 2018b). The Forest Service states that it is required to do a HERA and cannot rely solely on the EPA safety demonstration under FIFRA. According to the Forest Service, EPA often considers many forestry pesticide uses to be minor so the Forest Service must evaluate “the project-specific rates, spectrum of target and non-target organisms, and specialized exposure scenarios” in its HERA (USDA–FS, 2018c). Therefore, the Forest Service does evaluate the forest-specific impacts of pesticides for potential human and environmental impacts, which are a part of forest health and the ecosystem services a forest provides. However, the HERA is primarily a quantitative, classic risk assessment and does not encompass many ecosystem services, such as cultural services.

Regulation of Biological Control Agents to Address Forest Health

Biological control agents are another method to address the impacts of insect pests and pathogens on forest health. USDA regulates biocontrol agents under the “plant pest” provisions of the Plant Protection Act, which is the same program that regulates certain biotech plants and trees. A PPQ 526 permit is required “for the importation, interstate movement and environmental release of plant pests (plant feeding insects, mites, snails, slugs, and plant pathogenic bacteria, viruses, fungi, etc.), biological control organisms of plant pests and weeds, bees, parasitic plants and Federally listed noxious weeds” (USDA-APHIS, 2017d). Thus,

¹⁵If a biopesticide is imported into the United States, it also requires a permit issued by USDA under the Plant Protection Act.

all research involving a potential biocontrol agent that might be used in a forest, as well as the release of that biocontrol agent into the environment, requires a permit from USDA. The research permits are designed to ensure that the biocontrol agent does not escape and persist in the environment, and so the research is conducted in a highly controlled setting. The release permits are granted only after a thorough review and assessment of potential impacts in the environment. In addition to the plant pest analysis, USDA also conducts a biological assessment to comply with the Endangered Species Act and either an EA or an EIS to comply with NEPA. The scope of the NEPA analysis is the whole continental United States, and it considers cumulative effects. Compliance with NEPA for the release of a biocontrol agent is similar to complying with NEPA for a biotech plant. The analysis covers only some aspects of forest health and ecosystem services. According to USDA, it can take more than a decade to identify, rear, and test biocontrol agents intended to control invasive plants or insects (Rose, 2018).

Assisted Migration or Habitat Restoration of Tree Varieties

Another method to address forest health issues is to plant existing tree varieties in new locations or to restore the existing habitat with selectively bred, genetically improved tree varieties that are resilient to the threat. The planting of trees can occur in one of three different forest settings: (1) federally owned forests; (2) state-owned forests; or (3) privately owned lands. The ownership of the land is the critical factor in determining the regulatory oversight for those plantings.

For privately owned lands, the private landowner has no significant restrictions limiting what trees can be planted on his or her property unless the planting of the tree may harm a listed endangered species or its habitat, in which case the Endangered Species Act would apply (Shirey and Lamberti, 2010). In addition, the Plant Protection Act only applies if the plant species is either a noxious weed or plant pest or if the tree that is being moved or planted harbors a plant pest or a noxious weed. Thus, even an endangered tree can be planted outside its normal range if it is done on private land. This circumstance arises in the case of the endangered Florida torreya (*Torreya taxifolia*). Members of the Torreya Guardians¹⁶ are openly planting these trees in nonnative environments in 12 states, and the District of Columbia¹⁷ and those actions do not violate any federal law, nor is there any requirement to assess the impact of those new species on the forest health of the private lands where they are being planted. This circumstance would also apply to a biotech forest tree that did not fall within the regulatory authority of USDA (not a plant pest) or EPA (not a pesticide). For a biotech tree that is regulated by USDA, once the regulatory process has been satisfactorily completed, the biotech tree could be planted on privately owned land without triggering any other regulatory requirements or government policies. For a biotech tree regulated by EPA, EPA oversight continues after registration and conditions could be placed on how the tree is planted in the environment. It is anticipated, for example, that the biotech American chestnut tree will be reintroduced through plantings on private lands.

It is unclear if planting a nonnative tree species or planting a new variety of an existing tree on federal lands requires any special permit or regulatory review that assess the impact of the introduction on forest health. The Forest Service has a definition of “assisted migration,” which is a “management approach whereby resource managers physically move species (individuals, seeds, etc.) to new locations assessed suitable under changed climate conditions” (USDA-FS, n.d.). However, there does not seem to be any specific policy on the use of assisted migration on Forest Service lands (Millar, 2015). It also has a Native Plant Materials Policy and its Forest Service Manual has a chapter about “Vegetation Ecology” (USDA-FS, 2008). Those two policy documents give primary consideration to the planting of “genetically appropriate native plant materials” and restrict nonnative plant material use to limited conditions, such as emergency conditions to protect basic resource values, when native plant material is not available, or in highly altered plant communities, such as road cuts or log landings.

¹⁶See <http://www.torreyaguardians.org>.

¹⁷The District of Columbia, Florida, Georgia, Indiana, Massachusetts, Michigan, New Hampshire, North Carolina, Ohio, Oregon, Pennsylvania, Tennessee, and Wisconsin.

In 2016, the Forest Service finalized its Ecosystems Restoration Policy (USDA–FS, 2016:24785) to provide “broad guidance for restoring ecosystems on National Forest System lands so that they are self-sustaining and, if subject to disturbances or environmental change, have the ability to reorganize and renew themselves.” It specifies a science-based approach that the forest can be resilient for multiple uses. In particular, the policy states that when developing plans that include restoration, the Forest Service should include:

- a. Factors such as the following:
 1. public values and desires;
 2. that natural range of variation;
 3. ecological integrity;
 4. current and likely future ecological capabilities;
 5. a range of climate and other environmental change projections;
 6. the best available scientific information; and
 7. detrimental human uses.
 - b. technical and economic feasibility to achieve desired future conditions.
 - c. ecological, social, and economic sustainability....
 8. the social, economic, and ecological influences of restoration activities at multiple scales.
- (USDA-FS, 2016:24792)

Thus, this policy seems to require that the Forest Service consider a number of factors that fall within this report’s broad definition of forest health when deciding about restoring ecosystems affected by natural disturbances and climate change. Depending on how it is implemented, it could result in an analysis covering more comprehensively many of the ecosystem services provided by forests.

For lands managed by the U.S. Department of the Interior’s Fish & Wildlife Service (FWS), “there are no written guidelines or policy for introductions” within the historical range, augmentation of an existing population, and translocation (Johnson et al., 2013; Communication from the U.S. Fish & Wildlife Service, Washington, DC, to the National Academies of Sciences, Engineering, and Medicine’s Committee on the Potential for Biotechnology to Address Forest Health, March 2018). However, the planting of the trees would need to comply with the Endangered Species Act and the Migratory Bird Treaty Act. For National Wildlife Refuges, nonnative communities are not allowed unless there is no feasible alternative. In addition, the FWS has a Biological Integrity, Diversity and Environmental Health policy (FWS, 2001) for maintaining and restoring lands and waters in the National Wildlife Refuge System. That policy states that if there are lost or degraded areas, they should be restored to first mimic historic conditions and only use nonnative plant communities if there is no feasible alternative to accomplish the refuge’s purposes. The policy does allow for the use of genetically modified organisms but only if they are essential to accomplish refuge purposes and their use is approved by the Regional Chief (FWS, 2001).¹⁸

CONCLUSIONS AND RECOMMENDATIONS

Biotech trees developed to address forest health are regulated under the same statutes and regulations as any biotech plant. Forest health is not accounted for in the regulations for the use of biotechnology or for other approaches to mitigating forest tree insect pests or pathogens.

Conclusion: The current regulatory framework for biotech plants applies to biotech forest trees and does not impose any additional or different requirements for trees than other plants.

¹⁸In addition to the U.S. Forest Service and the U.S. Fish & Wildlife Service, there are other federal agencies that manage federal lands, such as the National Park Service, the Bureau of Land Management, and the U.S. Department of Defense. The committee did not investigate the policies of those agencies for how they would address different interventions to address a forest health issue.

The Coordinated Framework for the Regulation of Biotechnology, which was established in 1986, specified that oversight of biotechnology products would be carried out using existing legislative statutes. The same statutes utilized by USDA, EPA, and FDA to regulate biotech plants apply to biotech trees, including biotech trees designed to address forest health. There are no specific regulations or policies that those agencies apply to biotech trees.

Conclusion: The current regulatory framework that applies to biotech trees that are developed to address forest health encapsulates very few elements of the committee’s comprehensive definition of forest health.

If a biotech forest tree falls within the legal mandate of USDA, EPA, and/or FDA, then they regulate the tree the same as other biotech plants. USDA will conduct the necessary scientific risk analysis to ensure that the biotech tree is not a plant pest or noxious weed. EPA will carry out the different risk analyses to register the biotech tree’s pesticidal component, such as impacts on the environment as well as impacts on humans and other species. If a biotech tree has a food or feed component, such as a biotech chestnut, FDA will review any voluntary submission from the developer to alert them to any potential food or feed safety concerns. While some of the regulatory assessment procedures by USDA or EPA may cover a few aspects of forest health (such as impacts on nontarget species or impacts on soil or groundwater), those regulatory procedures do not consider most aspects of forest health when regulating a biotech tree.

Conclusion: If a regulatory agency is required to comply with the National Environmental Policy Act when regulating a biotech tree, then some components of forest health will be analyzed.

The National Environmental Policy Act (NEPA) requires that the federal government assess the environmental impact of its actions. To the extent that an agency regulating a biotech tree is required to conduct an EA or an EIS to comply with NEPA, some components of forest health will be analyzed before the government regulatory process is completed. That analysis is supposed to cover the “human environment,” which can include “ecological, aesthetic, historic, cultural, economic, social or health” effects. An analysis under NEPA must also comply with various Executive Orders, which encompass aspects of forest health (such as impacts on minority and low-income populations or consultations with tribal governments). However, out of the three agencies, only USDA undertakes the analysis required by NEPA for biotech plants. In addition, USDA cannot alter its regulatory decision based on the NEPA findings.

Conclusion: USDA only carries out a NEPA analysis—environmental assessment and/or environmental impact statement—for a small subset of biotech trees.

A review of the regulatory activity by USDA for biotech trees found that much biotech research (1,191 regulatory requests) has been carried out under USDA’s notification process, which does not require NEPA compliance. For biotech trees that have required a USDA permit to conduct research, only 4 percent of the 387 permits for biotech fruit and nonfruit trees required an EA and none required an EIS. For petitions to USDA for nonregulated status, for a large majority of those requests, USDA conducted an EA and not an EIS. USDA has completed nine EIS for its oversight of biotech plants out of approximately 124 petitions, and only one has been for a biotech tree (a frost-tolerant eucalyptus). Therefore, only a small fraction of USDA’s oversight of biotech trees involves a NEPA analysis.

Conclusion: As is the case with other biotech plants, some biotech trees could become commercial products without any oversight by the three regulatory agencies.

The three major statutes that regulate biotech plants do not necessarily require oversight for all biotech plant applications. If USDA determines that a biotech tree does not fall within its legal mandate to regulate potential “plant pests,” then the agency does not have any regulatory authority over the tree, does not carry

out any assessment, and the tree can be released into the environment without USDA's approval. In 2014, USDA made such a determination for a biotech loblolly pine and could make such determinations in the future for biotech trees where a gene was introduced using biolistics, if modifications to the genome are made with genome editing, or if no *Agrobacterium* DNA remains in the final product. EPA only has regulatory oversight if the tree produces a pesticide, and many biotech trees will not produce a pesticide. FDA's process is voluntary and only applies to plants that have food products or feed products, and many biotech forest trees may not have a food and/or feed use.

Conclusion: There are mechanisms in place to alert neighboring countries about biotech forest trees that could enter their territory, but biotech trees could migrate across a national border without notice if the biotech tree is not regulated in the country of origin.

If a biotech tree is regulated by USDA and/EPA, before a decision is made, notice is given both to the public as well as to neighboring countries. Similarly, if Canada regulates a biotech tree, federal regulators are made aware of their actions. The public notice and coordination mechanisms allow for proper compliance with regulatory requirements in the country in which the biotech tree might migrate. However, if the biotech tree is not regulated in the country of origin, then it could migrate to a neighboring country, potentially in noncompliance with that country's regulations.

Conclusion: Forest health also is not considered in the regulation of nonbiotech products designed to address forest health problems, such as biological control agents, pesticides, and assisted migration.

Other interventions to address forest health, such as pesticides, biological control agents, and assisted migration, also may require federal government review and oversight before deployment. When reviewing the regulatory processes for those interventions and the risk analysis conducted by the regulatory agency, the assessments or reviews conducted do not do a better job of incorporating forest health and ecosystem services into their analysis than the assessments conducted for biotech trees.

Conclusion: Some federal agencies have policies for the assisted migration of trees and/or the planting of biotech trees on federal lands while private landowners can plant nonnative and biotech trees without violating any federal laws or policies.

The Forest Service has some policies that apply to assisted migration and the planting of species to restore forest ecosystems. Those policies seem to consider some aspects of forest health in deciding whether to introduce or reintroduce a tree species. FWS has no policy for introductions within their historical range but does have a policy for maintaining and restoring lands and waters in the National Wildlife Refuge System. Private landowners can plant virtually any commercially available tree on their lands, whether a native species, a nonnative species, or a biotech tree.

Recommendation: Regulatory agencies should explore ways to incorporate into their regulatory oversight responsibilities the ability to assess the impact on ecosystem services for biotech and non-biotech products developed for improving forest health.

REFERENCES

Barnhill-Dilling, S.K. 2018. Engineered Governance: Public Engagement as a Path to Inclusive Environmental Governance in Genetically Engineered Trees. Ph.D. dissertation, North Carolina State University. Available at: <https://repository.lib.ncsu.edu/handle/1840.20/35317>. Accessed November 21, 2018.

- Campbell, F.T. 2018. Biotechnology? OK, But So Many More Issues Need to be Resolved. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine's Committee on the Potential for Biotechnology to Address Forest Health. Available at <http://nas-sites.org/dels/files/2018/02/Faith-Campbell-Presentation.pdf>. Accessed July 27, 2018.
- Carter, J. 1979. Exec. Order No. 12114. Environmental effects abroad of major federal actions. Federal Register 44:1957. Available at <https://www.archives.gov/federal-register/codification/executive-order/12114.html>. Accessed July 20, 2018.
- Clinton, W. J. 1994. Exec. Order No. 12898: Federal actions to address environmental justice in minority populations and low-income populations. Federal Register 59(32):7629–7633. Available at <https://www.archives.gov/files/federal-register/executive-orders/pdf/12898.pdf>. Accessed July 19, 2018.
- Clinton, W. J. 1997. Exec. Order No. 13045: Protection of children from environmental health risks and safety risks. Federal Register 62(78):19885–19888. Available at <https://www.gpo.gov/fdsys/pkg/FR-1997-04-23/pdf/97-10695.pdf>. Accessed July 19, 2018.
- Clinton, W. J. 2000. Exec. Order No. 13175: Consultation and coordination with Indian tribal governments. Federal Register 65(218): 67249–67252. Available at <https://www.gpo.gov/fdsys/pkg/FR-2000-11-09/pdf/00-29003.pdf>. Accessed December 12, 2018.
- Clinton, W. J. 2001. Exec. Order No. 13,186: Responsibilities of federal agencies to protect migratory birds. *Federal Register* 66(11):3853–3856. Available at https://www.energy.gov/sites/prod/files/nepapub/nepa_documents/RedDont/Req-EO13186migratorybirds.pdf. Accessed July 19, 2018.
- Costanza, A. 2018. Regulation of GE Trees in the U.S. and Beyond. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine's Committee on the Potential for Biotechnology to Address Forest Health. Available at <http://nas-sites.org/dels/files/2018/02/Adam-Costanza-Presentation.pdf>. Accessed July 27, 2018.
- Doley, B. 2018. Unintentional International Movement of GE Trees: Regulatory Response Scenarios. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine's Committee on the Potential for Biotechnology to Address Forest Health. Available at <http://nas-sites.org/dels/files/2018/02/Bill-Doley-Presentation.pdf>. Accessed July 30, 2018.
- EPA (U.S. Environmental Protection Agency). 2010. Biopesticides Registration Action Document: Coat Protein Gene of Plum Pox Virus. Available at https://www3.epa.gov/pesticides/chem_search/reg_actions/registration/decision_PC-006354_7-May-10.pdf. Accessed July 19, 2018.
- EPA. 2015. Proposed Registration Decision for the New Active Ingredient Papaya Ringspot Virus Resistance Gene (Papaya Ringspot Virus Coat Protein Gene) in X17-2 Papaya (OECD Unique Identifier: UFL-X17CP-6). Available at <https://www.regulations.gov/document?D=EPA-HQ-OPP-2015-0418-0005>. Accessed July 27, 2018.
- EPA. 2017. Current and Previously Registered Section 3 Plant-Incorporated Protectant (PIP) Registrations. Available at <https://www.epa.gov/ingredients-used-pesticide-products/current-and-previously-registered-section-3-plant-incorporated>. Accessed July 27, 2018.
- EOP (Executive Office of the President). 2016. National Strategy for Modernizing the Regulatory System for Biotechnology Products. Available at https://obamawhitehouse.archives.gov/sites/default/files/microsites/ostp/biotech_national_strategy_final.pdf. Accessed December 12, 2018.
- EOP. 2017. Modernizing the Regulatory System for Biotechnology Products: An Update to the Coordinated Framework for the Regulation of Biotechnology. Available at https://obamawhitehouse.archives.gov/sites/default/files/microsites/ostp/2017_coordinated_framework_update.pdf. Accessed July 19, 2018.
- FDA (U.S. Food and Drug Administration). 1992. Statement of Policy – Foods Derived from New Plant Varieties. Available at <https://www.fda.gov/Food/GuidanceRegulation/GuidanceDocumentsRegulatoryInformation/BioTechnology/ucm096095.htm>. Accessed July 19, 2018.
- FDA. 2017. AquAdvantage Salmon – Response to Public Comments on the Environmental Assessment. Available at <https://www.fda.gov/AnimalVeterinary/DevelopmentApprovalProcess/GeneticEngineering/GeneticallyEngineeredAnimals/ucm466220.htm>. Accessed July 20, 2018.
- FDA. 2018. Biotechnology Consultations on Food from GE Plant Varieties. Available at <https://www.accessdata.fda.gov/scripts/fdcc/?set=Biocon>. Accessed July 19, 2018.
- FWS (U.S. Fish & Wildlife Service). 2001. 601 FW 3: Biological Integrity, Diversity, and Environmental Health. Available at <https://www.fws.gov/policy/601fw3.pdf>. Accessed July 30, 2018.
- Gelvin, S.B. 2003. *Agrobacterium*-mediated plant transformation: The biology behind the “gene-jockeying” tool. *Microbiology and Molecular Biology Reviews* 67(1):16–37.
- Johnson, R., S. Boyce, L. Brandt, V. Erickson, L. Iverson, G. Kujawa, and B. Tkacz. 2013. Policy and Strategy Considerations for Assisted Migration on USDA Forest Service Lands. Proceedings of the 60th Annual Western

- International Forest Disease Work Conference; 2012 October 8-12; Tahoe City, CA. Available at https://www.fs.fed.us/nrs/pubs/jrnl/2013/nrs_2013_johnson_001.pdf. Accessed July 27, 2018.
- Millar, C. 2015. Assisted Migration for Forest Regeneration: Examples from Canada and a Bit on USFS Policy. Presentation at the meeting of the Consortium for Integrated Climate Research in Western Mountains on Assisted Migration Reforestation in Sierra Nevada Ecosystems. Available at https://www.fs.fed.us/psw/cirmount/meetings/AM2015/Millar_AM2015.pdf. Accessed July 30, 2018.
- NASEM (National Academies of Sciences, Engineering, and Medicine). 2016. Genetically Engineered Crops: Experiences and Prospects. Washington, DC: The National Academies Press.
- NASEM. 2017. Preparing for Future Products of Biotechnology. Washington, DC: The National Academies Press.
- OSTP (Office of Science and Technology Policy). 1986. Coordinated Framework for Regulation of Biotechnology. Available at https://www.aphis.usda.gov/brs/fedregister/coordinated_framework.pdf. Accessed July 19, 2018.
- Patterson, N. 2018. Haudenosaunee & the TG chestnut. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine Committee on the Potential for Biotechnology to Address Forest Health, March 2.
- Petermann, A. 2018. Genetically Engineered Trees. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine's Committee on the Potential for Biotechnology to Address Forest Health. Available at <http://nas-sites.org/dels/files/2018/02/Anne-Petermann-Presentation.pdf>. Accessed July 27, 2018.
- Rose, R. 2018. USDA, Animal and Plant Health Inspection Service, Plant Protection and Quarantine: Biological Control Permitting Overview. Webinar presentation to the National Academies of Sciences, Engineering, and Medicine's Committee on the Potential for Biotechnology to Address Forest Health. Available at <http://nas-sites.org/dels/files/2018/02/Robyn-Rose-Presentation.pdf>. Accessed July 27, 2018.
- Shirey, P.D., and G.A. Lamberti. 2010. Assisted colonization under the U.S. Endangered Species Act. *Conservation Letters* 3(1):45–52.
- Strauss, S. 2018. Why Biotech Solutions are Needed to Address Forest Health. Presentation to the National Academies of Sciences, Engineering, and Medicine's Committee on The Potential for Biotechnology to Address Forest Health. Available at <http://nas-sites.org/dels/files/2017/11/Steve-Strauss-Presentation.pdf>. Accessed July 27, 2018.
- USDA-APHIS (U.S. Department of Agriculture Animal and Plant Health Inspection Service). 2008. Perennials Statement. Available at https://www.aphis.usda.gov/brs/pdf/BRS_Perennials_Statement.pdf. Accessed July 19, 2018.
- USDA-APHIS. 2011. USDA-APHIS Biotechnology Regulatory Services User Guide: Notification. Available at https://www.aphis.usda.gov/biotechnology/downloads/notification_guidance_0311.pdf. Accessed July 19, 2018.
- USDA-APHIS. 2013. Questions and Answers: APHIS' Notice of Intent to Prepare an Environmental Impact Statement for Freeze Tolerant Eucalyptus Lines. Available at https://www.aphis.usda.gov/publications/biotechnology/2013/faq_brs_combined_petitions.pdf. Accessed July 19, 2018.
- USDA-APHIS. 2016. USDA-APHIS Biotechnology Regulatory Services Request to Extend Nonregulated Status from a Previous Determination: Extension Guidance for Developers. Available at https://www.aphis.usda.gov/brs/aphisdocs/guidance_ext_nonreg.pdf. Accessed July 19, 2018.
- USDA-APHIS. 2017a. ArborGen, Inc. Petition (11-019-01p) for Determination of Non-regulated Status for Freeze Tolerant Eucalyptus Lines FTE 427 and FTE 435: Draft Environmental Impact Statement – April, 2017. Available at https://www.aphis.usda.gov/brs/aphisdocs/11_01901p_peis.pdf. Accessed July 19, 2018.
- USDA-APHIS. 2017b. Check Status: Search APHIS BRS Permits and Notification Data. Available at https://www.aphis.usda.gov/aphis/ourfocus/biotechnology/permits-notifications-petitions/sa_permits/ct_status. Accessed July 19, 2018.
- USDA-APHIS. 2017c. Permits with Environmental Assessments. Available at <https://www.aphis.usda.gov/aphis/ourfocus/biotechnology/reports/ea-table>. Accessed July 19, 2018.
- USDA-APHIS. 2017d. Regulated Organism and Soil Permits. Available at <https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/permits/regulated-organism-and-soil-permits>. Accessed July 20, 2018.
- USDA-APHIS. 2017e. USDA-APHIS Biotechnology Regulatory Services Permit User's Guide with Special Guidance for ePermits. Available at https://www.aphis.usda.gov/biotechnology/downloads/permit_guidance.pdf. Accessed July 19, 2018.
- USDA-APHIS. 2018a. BRS Interstate/Release and Release Permits and Notifications. Available at https://www.aphis.usda.gov/aphis/ourfocus/biotechnology/permits-notifications-petitions/sa_permits/status-update/release-permits. Accessed July 19, 2018.
- USDA-APHIS. 2018b. Petitions for Determination of Nonregulated Status. Available at <https://www.aphis.usda.gov/aphis/ourfocus/biotechnology/permits-notifications-petitions/petitions/petition-status>. Accessed July 19, 2018.
- USDA-APHIS. 2018c. Regulated Article Letters of Inquiry. Available at https://www.aphis.usda.gov/aphis/ourfocus/biotechnology/am-i-regulated/regulated_article_letters_of_inquiry/regulated_article_letters_of_inquiry. Accessed July 19, 2018.

- USDA-FS (U.S. Department of Agriculture U.S. Forest Service). 2008. Forest Service Manual, National Headquarters (WO), Washington, DC. FSM 2000 – National Forest Resource Management. Chapter 2070 – Vegetation Ecology. Available at https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_066309.pdf. Accessed July 30, 2018.
- USDA-FS. 2013. Forest Service Manual, National Headquarters (WO), Washington, DC. FSM 2100 – Environmental Management. Chapter 2150 – Pesticide Use Management and Coordination. Available at https://www.fs.fed.us/dirindexhome/fsm/2100/wo_2150.doc. Accessed July 20, 2018.
- USDA-FS. 2016. Ecosystem Restoration Policy. Federal Register 81(81):24785–24793. Available at <https://www.gpo.gov/fdsys/search/pagedetails.action?granuleId=2016-09750&packageId=FR-2016-04-27&acCode=FR&collectionCode=FR>. Accessed July 30, 2018.
- USDA–FS. 2018a. Pesticide Management & Coordination. Available at <https://www.fs.fed.us/foresthealth/protecting-forest/integrated-pest-management/pesticide-management/>. Accessed July 20, 2018.
- USDA-FS. 2018b. Pesticide Management & Coordination: Health & Safety. Available at <https://www.fs.fed.us/foresthealth/protecting-forest/integrated-pest-management/pesticide-management/pesticide-health-safety.shtml>. Accessed July 20, 2018.
- USDA-FS. 2018c. Pesticide Management & Coordination: Risk Assessments. Available at <https://www.fs.fed.us/foresthealth/protecting-forest/integrated-pest-management/pesticide-management/pesticide-risk-assessments.shtml>. Accessed July 20, 2018.
- USDA-FS. n.d. Climate Change Resource Center: Management Options FAQ's. Available at <https://www.fs.usda.gov/ccrc/climate-basics/climate-faq/management-options>. Accessed July 30, 2018.

Moving Ahead

Biotechnology has the potential to help mitigate threats to North American forests from insect pests and pathogens through the introduction of pest-resistant traits. However, it also presents some challenges. The necessary genetic changes to achieve resistance are often not easy to identify and are challenging to implement. Tree genomes are complex, and much remains to be learned about the genetic mechanisms that underlie important traits. Most resistance traits are thought to be polygenic, controlled by many loci, in theory, potentially hundreds, each of which may have small genetic effects and complex epistatic interactions (Boyle et al., 2017). Additionally, unlike the modification of agricultural crops through biotechnology—in which a genetic change is introduced to and propagated in an individual cultivar or variety—genetic changes incorporated into trees for forest health purposes need to be introduced into diverse breeding populations so that tree species can respond to biotic and abiotic stress over time and across their spatial distributions.

Furthermore, the effectiveness of biotechnology at mitigating forest threats needs to be assessed on many fronts. In addition to evaluating the utility of the resistance trait in protecting a tree species, the modified tree needs to be tested for viability in the diversity of environments in which it will live. An assessment of the effects of the tree on other species in the environment (including humans) is also important, as is a comparison of using biotechnology to address the threat versus using other mitigation tools.

Finally, research and investment efforts need to be made in areas besides biotechnology, including the development of further strategies for preventing the introduction of nonnative insects and pathogens, human capital development in professions related to tree breeding, and social science research, including on a conceptual framework for capturing and accounting for the intrinsic value of forests. Such work will benefit the health of forests, regardless of the pest mitigation tools put to use.

Therefore, the committee recommends research and investment on three fronts to address knowledge gaps about the application of biotechnology to mitigate threats to forest health and to improve its utility as a forest health tool:

1. Knowledge about tree genetics related to resistance,
2. Data and tools for impact assessment, and
3. Management approaches that take into account disciplines beyond biotechnology.

The recommendations from the chapters are restated here along with a few additional recommendations to support a holistic effort to improve forest health.

IMPROVING THE EFFECTIVENESS OF BIOTECHNOLOGY

Technical constraints and lack of basic information (Scheben and Edwards, 2017) may provide significant challenges to fully utilizing biotechnology in many tree species in the near future. Understanding of the genomes of North American tree species is inadequate given the number of species under threat, insufficient knowledge exists about the fundamental mechanisms involved in resistance to pests to efficiently identify genomic means to mitigate pest damage, and the combination of genes that respond to pest outbreaks is poorly understood in most forest tree species. A thorough knowledge of tree genomes would

provide access to a suite of technologies that could contribute to forest health initiatives, such as gene discovery, gene expression profiling, and genome editing.

Once the mechanisms of resistance are understood, researchers will need to ensure that modified trees include the genetic diversity necessary for survival over long generation times in diverse and changing environmental conditions. Biotechnology could be used in combination with selective-breeding programs for tree species at risk to ensure that sufficient genetic diversity is retained in the resistant trees. Biotechnology tools (e.g., transgenesis or genome editing) would be used to insert one or more resistance genes into relatively few tree genotypes, and these trees would become the parent trees in a seed orchard from which resistant seed could be produced. This process is similar to that of selective-resistance breeding, where a finite number of parent trees with documented genetic resistance are placed into seed orchards to produce the seed required for restoration or reforestation goals.

A limitation of selective breeding is the time it can take to combine different resistance genes or to deliver a high percentage of orchard seed that will produce resistant seedlings. For some tree species (e.g., sugar pine, *Pinus lambertiana*), it may take 10 to 20 years to breed trees with different combinations of resistance genes. Biotechnological tools may be able to combine resistance genes in a much shorter period of time or to combine resistance genes not found in the tree species of interest with resistance genes that are already present in the species. The combination of precision phenotyping to identify trees in the field that express pest resistance, selective breeding, and biotechnological methods could be synergistic in speeding up tree improvement efforts while still ensuring success in the long term. A combined approach may be particularly advantageous when stacking qualitative (notably single-gene) resistance with quantitatively inherited resistance. Seed orchards containing parent trees with qualitative and quantitative resistance (either in the same individual or in different individuals), would produce seed that has qualitative resistance and a varied mix of quantitative resistance.

To address forest health, genetic resistance in trees needs to be durable over hundreds of years. Populations of trees with several types of resistance, including a mix of qualitative and quantitative resistance, would have the best chance of meeting this durability goal. Sustaining forest tree populations over the long term will also require combining durable resistance with a diverse array of genetic backgrounds locally adapted to their microgeographic environments. Provenance tests, ecological niche modeling, and precision phenotyping across multiple ecological niches will shed light on the extent of the locally adapted standing genetic variation present along the wide geographical distribution of a species. Understanding the relationship of spatial distributions, genetic diversity, and local adaptation is essential for determining the genetic backgrounds against which to deploy a biotech tree to ensure that the breeding program is capturing the maximum possible genetic variation within the species of interest.

Identifying resistance in selectively bred trees usually includes both a relatively fast seedling assay (e.g., artificial inoculation of young seedlings with spores of the pathogen that causes white pine blister rust and evaluation/phenotyping of thousands of seedlings for resistance) and extensive field testing to examine the efficacy of genetic resistance in a range of environments and over time. Any biotechnological resistance introduced in one or more individuals would need to go through one or both of these steps. At the time the committee was writing its report, regulation of field trials of biotech forest trees restricted flowering to guard against unintended gene flow. Caution may be warranted on a case-by-case basis because of the risk of spread of biotech forest trees prior to completion of the initial impact assessment (intended to be informed by field trials). Additionally, modeling and other approaches should be developed to address questions of gene flow, dispersal, long-term performance of resistance in biotech forest trees, and the establishment of and interactions of these trees with other components of the environment.

Recommendations

- **Sufficient investment of time and resources should be made to successfully identify or introduce resistance into tree species threatened by insects and pathogens.**
- **More research should be conducted on the fundamental mechanisms involved in trees' resistance to pests and adaptation to diverse environments, including a changing climate.**

- The deployment of any biotechnological solution with the goal of preserving forest health should be preceded by developing a reasonable understanding in the target species of (a) rangewide patterns of distribution of standing genetic variation including in the putative glacial refugia, if known; (b) magnitude of local adaptation (*gene × environment* relationships); and (c) identification of spatial regions that are vulnerable to genetic offset.
- Entities concerned about forest health should devote resources to identifying resistant trees within a population that have survived a pest outbreak. Research to understand the role of resistance in coevolved systems from the perspective of a global host–pest system, where the nonnative pathogen or insect originates, would help guide efforts in North America.
- Research should address whether resistance imparted to tree species through a genetic change will be sufficient to persist in trees that are expected to live for decades to centuries as progenitors of future generations.

IMPROVING IMPACT ASSESSMENT

The timely development of an impact assessment framework is critical. Developing the process for incorporating the risk of ecosystem service loss, including cultural, aesthetic, and nonuse values, and comparing that risk with alternative approaches to address pest threats to tree species will require substantial effort. As more is learned about impacts (positive and negative) of different interventions for forest health over time, the approach can be adaptively modified.

The longevity of trees and the large spatial scales involved in mitigating threats to tree species from pests means that predictive modeling will be needed to evaluate the potential success of using biotechnology to confer pest resistance and to design the outplanting approach to best facilitate gene flow. Uncertainty analysis of model parameters will direct specific research and indicate monitoring needs. While model parameterization will vary by species, geography, and the traits under consideration, development of criteria for these models should be an early research focus. Evaluation of some elements of the impact assessment will only be possible via modeling.

Incorporation of climate change scenarios into modeling efforts would improve the design for species restoration efforts by explicitly representing uncertainty about the suitability of habitats in the future. It would be useful to model climate change scenarios whether resistant trees to be planted are developed using biotechnology or selective breeding. Climate change will influence both pest and tree distributions and pest impacts. Research will be needed to refine these predictions by species over time.

Further, if the decision is made to go ahead with outplanting a biotech tree, a full monitoring and assessment plan should be developed so that ample learning takes place from these initial efforts. The knowledge gained can then be used to adaptively refine both the decision-making approach and the impact framework. For example, field testing of seedlings should reveal both the movement and durability of resistant genes through a tree population. These data will help with evaluation of whether the next generations of the species will propagate resistance through natural regeneration as intended and whether other traits have been modified with the addition of resistance. Where flowering trials are permitted, results would inform both impact assessment and modeling to predict the consequences of large-scale deployment. Focused research and tracking of early biotech species should improve decision making about other species under consideration for biotechnological solutions. Adaptive management that facilitates a stepwise approach to data gathering on gene flow and other impacts at different spatial and temporal scales would be useful for achieving the goal of addressing forest health.

Forest health is not currently considered in the federal regulatory assessments of approaches to mitigate forest health threats, whether or not those approaches use biotechnology. The committee was not tasked with suggesting changes to the U.S. regulatory system, but it thinks that the regulatory agencies of biotech plants—particularly the U.S. Department of Agriculture and the U.S. Environmental Protection Agency—could explore whether an assessment of impacts on ecosystem services could be incorporated into their oversight responsibilities. Such assessments should be done for all approaches designed to address forest health, not just biotechnology.

Recommendations

- **Federal agencies should continue efforts to improve the incorporation of all components of ecosystem services into the integrated impact assessment.**
- **Modeling and other approaches should be developed to address questions about biotech tree gene flow, dispersal, establishment, performance, and impact that are precluded where flow-
ering of field trial material is restricted.**
- **Models for tree biotech impact assessments should identify, quantify, and account for sources of uncertainty.**
- **An adaptive management approach to forest health should be used to ensure continued learning and address impacts to both the environment and society.**
- **Impact assessment should be a continuous and iterative process.**
- **Regulatory agencies should explore ways to incorporate into their regulatory oversight responsibilities the ability to assess the impact on ecosystem services for biotech and non-biotech products developed for improving forest health.**

RESEARCH AND INVESTMENT NEEDS BEYOND BIOTECHNOLOGY

Biotechnology is one of many approaches to addressing forest health and should not be pursued to the exclusion of other forest health management options, including prevention and site management practices. Substantial literature supports the need for sustained investment in prevention and eradication as the most cost-effective and lowest impact approaches for managing introductions of nonnative insect pests and pathogens. Where these efforts fail or when native pests and pathogens are involved, multiple management options may be needed. Many responses will likely require integrated approaches for positive impact. Amplifying existing or introduced genetic resistance of the host species through breeding is an essential element for mitigating the impacts of introduced pathogens or insects. Several ongoing breeding programs reviewed in Chapter 3 give reason for optimism about the feasibility of this approach, and new technologies may increase their efficiency in the future. All management approaches will require sustained resources because eradication of widespread infestations has low probability, insect pests and pathogens can evolve over time, reintroduction of insect pests and pathogens is likely, and some options require decades for successful development and deployment. Continuing efforts to track the import of new pests, the spread of existing native and nonnative pests, and the potential evolution of pests in response to both increased resistance and other drivers will also be necessary to ensure that any management effort is consistent with the current and expected threat.

To be used successfully as a tool for mitigating forest health threats, biotechnology needs to be integrated into selective-breeding programs to capture existing genetic diversity. However, many forest tree species under severe pest attack do not have adequate and sustained breeding programs. Furthermore, the capacity of selective-breeding programs in U.S. institutions has been severely eroded since the mid-20th century (Wheeler et al., 2015). Human capital will be needed in the professions of tree breeding genetics, computational biology, forest pathology and entomology, tree physiology, invasion biology, biogeography, forest economics, and rural sociology to guide the development and potential deployment pest-resistant trees effectively. Research training is available in most of these disciplines at many public institutions, but they seldom operate under a cohesive theme. To train future scientists with the expertise needed to address forest health threats, institutions may want to consider undertaking cluster hires of faculty from each of these disciplines to foster collaborative multidisciplinary research in these areas. They could also create multidisciplinary graduate programs to provide professional training in two or more of these disciplines. Furthermore, many biologists still receive little training in computational science. Making such training part of graduate programs in forest-related disciplines will go a long way toward development of strong quantitative skills in professionals dealing with large datasets (Spengler, 2000).

Interventions to address forest health using biotechnology should be evaluated not only as a matter of technical feasibility but also as relevant to social values. The impact assessment framework as proposed in Chapter 5 aims to reflect this inclusive approach, but there are challenges to the adequacy of its treatment of these considerations. Recent research on public attitudes in a variety of countries, although currently very limited, suggests some openness to using biotechnology to alter trees. However, ongoing controversy over the use of biotechnology in agricultural crops demonstrates that significant concerns exist among segments of society. Accordingly, these views should be recognized as important parts of the public dialogue about the potential for the use of biotechnology to address forest health.

Forests, especially noncommercial ones, are often associated with values such as naturalness, wildness, integrity, authenticity, sense of place, and place bonding, and they provide critical habitat for intrinsically valued and iconic species such as northern spotted owls. Biotechnological interventions may, on the one hand, be regarded as potentially undermining values such as naturalness, wildness, or integrity in forests and may also tap into more basic and unacknowledged disapproval of the management of forests (Hall, 2007; Gamborg and Sandøe, 2010). Alternatively, such interventions may be perceived as offering hope to preserve threatened species, much loved and culturally significant places, and valued ecosystems from the substantial changes that could follow the loss of a foundation species such as the whitebark pine.

The lack of clarity about how such values are likely to be interpreted and prioritized in the context of biotechnological interventions into forest health means that more studies of societal responses are needed. Studies should investigate how different cultural groups are likely to respond to the deployment of biotechnology for forest health, how stable and consistent these responses are, how they are related to deeper value orientations, and how they are affected by changes in knowledge about the technology. Whether some biotechnological strategies are generally thought more acceptable than others (for instance, whether cisgenesis is more acceptable than transgenesis, or whether genome editing is more acceptable where it does not involve transgenesis); and how people think about trade-offs between environmental values, such as the loss of some wildness value to protect an endangered species, should also be investigated.

Biotechnical interventions for forest health are likely to impose varying risks, costs, and benefits on different human groups over time, in particular on indigenous peoples. Where the development and deployment of biotech trees is being considered, these social impacts should be investigated, research into the perspectives of individuals and communities likely to be affected should be carried out, and affected communities should be engaged transparently and respectfully.

To take these concerns meaningfully into account, a conceptual framework is needed to complement impact assessment based on ecosystem services. This framework should take into account the ways that forests are valued intrinsically, spiritual and ethical concerns about the impacts of biotechnology on forests, and concerns about social justice related both to the impacts of biotech trees on diverse communities and the involvement of these communities in decision-making processes.

Visions of informed decision making and democratic governance associated with forest health threats and emerging technologies must go well beyond just educating people with scientific facts. Instead, policy makers must gain trust and connect with the different beliefs, values, and priorities that various groups of people hold (Brossard and Nisbet, 2006; Hajjar and Kozak, 2015). Spaces need to be created to initiate meaningful dialogue where diverse viewpoints and values can be brought together, concerns and past hardships can be expressed, and perceptions can be understood (Kleinman et al., 2011; Hajjar et al., 2014). One strategy for fostering this meaningful deliberation is to discuss risks in connection with benefits, although these issues are challenging to measure and represent in quantitative impact assessments or as part of models measuring various ecosystem services. Other approaches that respect and integrate local knowledge and mesh with local cultures of decision making may also hold promise. Regardless of the method, for engagement to matter, policy makers and technical experts must be open to reconsidering and possibly modifying their understandings and plans for action.

Recommendations

- Investment in effective prevention and eradication approaches should be the first line of defense against non-native species in efforts to maintain forest health.
- Management for forest health should make use of multiple practices in combination to combat threats to forest health.
- Public funders should support and expand breeding programs to encompass the genetic diversity needed to preserve tree species essential to ecosystem services.
- Investment in human capital should be made in many professions, including tree breeding, forest ecology, and rural sociology, to guide the development and potential deployment pest-resistant trees.
- More studies of societal responses to the use of biotechnology to address forest health threats in the United States are needed. Such studies might investigate (1) the responses of different social and cultural groups to the deployment of biotechnology in forests, (2) the stability and consistency of attitudes toward different applications of biotechnology in a range of circumstances, (3) differences in attitudes toward biotechnology strategies (e.g., cisgenesis, transgenesis, genome editing), (4) the relationship between deeper value orientations and attitudes toward biotechnology, and (5) how people consider trade-offs between values such as wilderness and species protection.
- Studies of societal responses to the use of biotechnology to address forest health threats should be used to help in developing a complementary framework to ecosystem services that takes into account intrinsic values, related spiritual and ethical concerns, and social justice issues raised by the deployment of biotechnology in forests.
- Respectful, deliberative, transparent, and inclusive processes of engaging with people should be developed and deployed, both to increase understanding of forest health threats and to uncover complex public responses to any potential interventions, including those involving biotechnology. These processes, which may include surveys, focus groups, town hall meetings, science cafés, and other methods, should contribute to decision making that respects diverse sources of knowledge, values, and perspectives.
- Developers, regulators, and funders should experiment with analytical-deliberative methods that engage stakeholders, communities, and publics.

REFERENCES

- Boyle, E.A., Y.I. Li, and J.K. Pritchard. 2017. An expanded view of complex traits: From polygenic to omnigenic. *Cell* 169(7):1177–1186.
- Brossard, D., and M.C. Nisbet. 2006. Deference to scientific authority among a low information public: Understanding U.S. opinion on agricultural biotechnology. *International Journal of Public Opinion Research* 19(1):24–52.
- Gamborg, C., and P. Sandøe. 2010. Ethical considerations regarding genetically modified trees. Pp. 163-175 in *Forests and Genetically Modified Trees*, Y.A. El-Kassaby and J.A. Prado, eds. Rome, Italy: Food and Agriculture Organization of the United Nations.
- Hajjar, R., and R.A. Kozak. 2015. Exploring public perceptions of forest adaptation strategies in Western Canada: Implications for policy-makers. *Forest Policy and Economics* 61:59–69.
- Hajjar, R., E. McGuigan, M. Moshofsky, and R.A. Kozak. 2014. Opinions on strategies for forest adaptation to future climate conditions in western Canada: Surveys of the general public and leaders of forest-dependent communities. *Canadian Journal of Forest Research* 44(12):1525–1533.
- Hall, C. 2007. GM technology in forestry: Lessons from the GM food 'debate.' *International Journal of Biotechnology* 9(5):436–447.
- Kleinman, D.L., J.A. Delborne, and A.A. Anderson. 2011. Engaging citizens: The high cost of citizen participation in high technology. *Public Understanding of Science* 20(2):221–240.
- Scheben, A., and D. Edward. 2017. Genome editors take on crops. *Science* 355(6330):1122–1123.
- Spengler, S.J. 2000. Bioinformatics in the information age. *Science* 287(5456):1221–1223.
- Wheeler, N.C., K.C. Steiner, S.E. Schlarbaum, and D.B. Neale. 2015. The evolution of forest genetics and tree improvement research in the United States. *Journal of Forestry* 113(5):500–510.

Glossary

Adaptive management	An iterative decision-making process in which scientific design and monitoring are integrated into management applications to systematically test assumptions in order to learn, reduce uncertainty, adapt to achieve the management objective.
Allele	One of the variant forms of a gene at a particular location (that is, locus) on a chromosome. Different alleles produce variation in inherited characteristics, such as blood type.
Assisted migration	<p>The physical movement of species (e.g., individuals or seeds) by humans to new locations assessed to be suitable under changed climate or other environmental conditions.</p> <p>These locations may potentially be sites that have hosted other seed sources of the species, or new environments.</p>
Backcross	The breeding of a hybrid organism with one of its parents or with an organisms genetically similar to a parent.
Biocontrol	See “Biological control.”
Biolistics	A technique that inserts DNA into plant cells by physical bombardment.
Biological control	The reduction of pest populations through the use of natural enemies such as parasitoids, predators, pathogens, antagonists, or competitors, to suppress pest populations.
Biotech tree	A tree whose genome has been modified by a biotechnological approach.
Biotechnology	A number of genetic modification methods other than selective breeding and sexually crossing organisms to endow new characteristics in organisms. These methods include transgenesis, cisgenesis, RNA interference, genome editing, and insertion of synthetic DNA to modify an organism’s DNA.
Cisgenesis	The insertion of endogenous gene(s) or DNA fragments from a sexually compatible species into cells of a target species to create a new gene sequence.
Conspecific	Organisms belonging to the same species.
Ecosystem services	Goods and services that are of value to people, provided wholly or in part by ecosystems.
Fitness	See “Genetic fitness.”
Forest health	A condition that sustains the structure, composition, processes, function, productivity, and resilience of forest ecosystems over time and space. An assessment of this condition is based on the current state of knowledge and can be influenced by human needs, cultural values, and land management objectives.
Foundational species	Species that exert a strong influence on other species and on ecosystem structure and function.

Gene flow	The transfer of genetic information from one population into another population (via pollen or propagules in plants).
Genetic fitness	A description of the ability to survive and reproduce, equal to the long-term average contribution to the gene pool by individuals having a particular genotype or phenotype.
Genetic offset	A metric that identifies populations within a species' distribution where local adaptation (<i>gene</i> × <i>environment</i> relationship) is most likely to be disrupted due to abiotic factors (e.g., climate change).
Genetic resistance	The ability of an organism to exclude or overcome (to some degree or completely) the damaging effect of a pest.
Genome	The complete sequence of the DNA in an organism.
Genome editing	Specific modification of the DNA of an organism to create mutations or introduce new alleles or new genes. The four main classes of this approach are meganucleases, zinc finger nucleases, transcription activator-like effector nucleases (TALENs), and the clustered regularly interspaced short palindromic repeat (CRISPR) nuclease system.
Genotype	All or part of the genetic constitution of an individual or group.
Heterozygous	For diploid organisms, having two different alleles for a specific locus.
High-impact species	Pest species that cause some combination of tree mortality, canopy thinning, growth loss, defoliation, and decreased reproduction or regeneration that significantly alters host population dynamics.
Homozygous	For diploid organisms, having two identical alleles for a specific locus.
Horizontal gene transfer	Movement of genes between populations of otherwise distinct species.
Hybridization	The breeding of genetically unlike parents usually of closely related species to produce offspring.
Hypovirulence	A kind of biological control in which the virulence of a pathogen is reduced by being infected with a virus.
Instrumental value	The value of things measured by their usefulness to humans and human welfare.
Intercross	The breeding of two organisms that are heterozygous.
Intrinsic value	The value of things as ends in themselves, regardless of whether they are also useful as means to other ends and independent of their usefulness to humans.
Invasive species	A species whose introduction does or is likely to cause economic or environmental harm or harm to human, animal, or plant health.
Keystone species	A species whose influence on ecosystem function and diversity is disproportionate to its numerical abundance.
Local adaptation	Adaptation of a population to the local environment where it has highest fitness compared to in other areas of the distribution range.
Marker-assisted selection	The use of polymorphic DNA sequences to enhance the efficiency of breeding.
Mast	The nuts, seeds, buds, and fruits produced by forest trees.

Noninstrumental value	See “Intrinsic value.”
Oomycetes	Fungus-like eukaryotic microorganisms that occupy saprophytic and pathogenic lifestyles. Many are plant pathogens, causing diseases such as seedling blights, damping-off, root rots, and foliar blights.
Outcross	The breeding of two organisms of the same species that are genetically unrelated.
Outplant	The action of planting trees in field conditions.
Pest	Insects and pathogens that cause damage to forest trees.
Phenology	The study of cyclic and seasonal natural phenomena, especially in relation to climate and plant and animal life. For plants, phenology refers to the study of effects of growth and development with specific timing such as flowering, bud set, bud break, and reproduction.
Phenotype	The observable characteristics of an organism (i.e., how it appears outwardly and physiologically) resulting from the interaction of genotype and the environment.
Phylogeography	The study of historical processes that may be responsible for contemporary geographic distributions of genealogical lineages.
Polygenic	A trait that is controlled by a multiple genes.
Provenance	The specified location from which plants and their propagules were derived, comprising the environment to which they may be locally adapted.
Qualitative resistance	Host genotypes show a discontinuous range of variation in resistance. Susceptible and resistant genotypes can be easily discerned, influenced by one or more genes of major effect.
Quantitative resistance	Host genotypes show a continuous range of variation in resistance from extremely susceptible to fairly resistant, influence by many minor genes.
Quantitative trait locus	A region of the genome that contributes to a phenotype in a quantitative manner.
RNA interference	A natural mechanism found in nearly all organisms in which the levels of transcripts are reduced or suppressed.
Selective breeding	Modification of the genetic constitution of a plant through sexually crossing different genomes and selecting desirable genotypes to serve as parental lines in subsequent generations.
Silviculture	The art and science of controlling the establishment, growth, composition, health, and quality of forests and woodlands to meet diverse needs and values.
Synthetic DNA	Genes produced in the laboratory that are not based on any naturally occurring DNA sequences but that may have functional properties or utility for genetic engineering.
Transgenesis	The insertion of foreign genes or DNA fragments into cells of a target species to create a new gene sequence.
Virulence	The degree of damage or pathogenicity caused by a pathogen to a host species.

Appendix A

Biographical Sketches of Committee Members

Chair

Dr. Susan E. Offutt is currently a senior consultant to the Global Strategy to Improve Agricultural and Rural Statistics at the UN Food and Agriculture Organization. Until her retirement from federal service in 2015, she was chief economist at the U.S. Government Accountability Office (GAO) for 8 years. Before joining GAO, she served as administrator of the U.S. Department of Agriculture's (USDA's) Economic Research Service for 10 years. Prior to that, she was executive director of the National Academies of Sciences, Engineering and Medicine's Board on Agriculture, which conducts studies on a range of topics in agricultural science. She was chief of the Agriculture Branch at the Office of Management and Budget (OMB). During her tenure at OMB, she coordinated budget and policy analysis of the farm bill and trade negotiations in addition to the operations of USDA. She began her career on the faculty at the University of Illinois at Urbana-Champaign, where she taught econometrics and public policy. She is a fellow of the American Applied Economics Association and the National Academy of Public Administration. She received an M.S. and a Ph.D. in agricultural economics from Cornell University.

Members

Dr. Vikram E. Chhatre is currently a senior research scientist with the IDeA Networks for Biomedical Research Excellence (INBRE) Bioinformatics Core at the University of Wyoming, where he helps biologists incorporate high-performance computing in their research. He is a forest population geneticist interested in understanding the demographic and evolutionary forces shaping the genetic structure of natural populations of tree species. Dr. Chhatre's research during the past 15 years has addressed issues in population, conservation, and quantitative genetics of long-lived and ecologically and economically important forest tree species such as spruce, pine, and poplar. Most recently he investigated the importance of range context and interspecific hybridization in understanding adaptation to climate in *Populus*, a model species and emerging bioenergy system. In the pursuit of these goals, he applies computational tools to genomic data obtained from next-generation sequencing technologies. Dr. Chhatre received a Ph.D. in genetics from Texas A&M University and was a postdoctoral fellow with the U.S. Department of Agriculture's Forest Service and the University of Vermont.

Dr. Jason A. Delborne is an associate professor of science, policy, and society in the Department of Forestry and Environmental Resources at North Carolina State University. Dr. Delborne joined the university in August 2013 as part of the Chancellor's Faculty Excellence Program in Genetic Engineering and Society. His research focuses on highly politicized scientific controversies, such as agricultural and forest biotechnology, gene drives, synthetic biology, and biofuels. Drawing upon the highly interdisciplinary field of science, technology, and society (STS), he engages various qualitative research methodologies to ask questions about how policy makers and members of the public interface with controversial science. Dr. Delborne holds a bachelor's degree in human biology from Stanford University (1993) and a doctorate in environmental science, policy, and management from the University of California, Berkeley (2005). He completed postdoctoral training funded by the National Science Foundation at the University of Wisconsin–Madison.

(2006–2008) before beginning his faculty career as an assistant professor of liberal arts and international studies at the Colorado School of Mines (2008–2013). Dr. Delborne recently served on the National Academies of Sciences, Engineering, and Medicine’s Committee on Gene Drive Research in Non-Human Organisms, which released its report *Gene Drives on the Horizon* in June 2016.

Dr. Stephen DiFazio is a professor in the Department of Biology and the director of the Genomics Core Facility at West Virginia University. His thesis research focused on gene flow and reproductive biology of conifers and cottonwoods. He then worked as a staff scientist at Oak Ridge National Laboratory, focusing on a variety of functional and structural genomics projects, most notably the sequencing of the *Populus* genome. He currently serves on many scientific advisory boards, including those of the National Science Foundation Plant Genome Project, Greenwood Resources, and the Forest Health Initiative. Dr. DiFazio received his B.S. in biology and English from Northeastern University and his M.S. in ecology and Ph.D. in forest genetics from Oregon State University.

Dr. Doria R. Gordon is a lead senior scientist, with a focus on ecosystems, in the Office of the Chief Scientist at the Environmental Defense Fund (EDF). Prior to EDF, she spent 25 years working in science, conservation, and management for The Nature Conservancy in Florida. Dr. Gordon is also a courtesy professor of biology at the University of Florida and a research associate at Archbold Biological Station near Lake Placid, Florida. She has conducted research on the restoration of forested ecosystems, including blue oak woodlands in California and longleaf pine systems in Florida. She has also developed and evaluated risk-assessment tools for predicting invasiveness in plant species. Dr. Gordon completed an M.S. and a Ph.D. in plant ecology at the University of California, Davis, following an undergraduate degree in biology and environmental studies at Oberlin College.

Dr. Inés Ibáñez is an associate professor in the School for Environment and Sustainability at the University of Michigan. Dr. Ibáñez’s research aims at developing the knowledge and the experimental and analytical frameworks necessary to generate near-term predictions of the effects of global change on forest ecosystems. Her work integrates existing knowledge and data into forecasting ecosystems’ dynamics under future environments. Outcomes from her work are geared at informing management decisions that optimize conservation, restoration and sustainable practices for a wide range of ecosystems varying from natural areas to tree plantations and urban vegetation. She received her B.S. in biology (botany) from Universidad Complutense de Madrid, an M.S. in range sciences from Utah State University, and a Ph.D. in ecology from Duke University.

Mr. Gregory Jaffe is the director of the Project on Biotechnology for the Center for Science in the Public Interest (CSPI). Mr. Jaffe came to CSPI after serving as a trial attorney for the U.S. Department of Justice’s Environmental and Natural Resources Division and as senior counsel with the U.S. Environmental Protection Agency’s Air Enforcement Division. He is a recognized international expert on agricultural biotechnology and biosafety and has published numerous articles and reports on those topics. He has worked on biosafety regulatory issues in the United States and throughout the world, including the African countries of Kenya, Uganda, Tanzania, Mali, Ghana, Malawi, South Africa, Burkina Faso, and Nigeria. He was a member of the U.S. Secretary of Agriculture’s Advisory Committee on Agricultural Biotechnology and 21st Century Agriculture from 2003 to 2008 and was reappointed to a new term from 2011 to 2016. He was also a member of the U.S. Food and Drug Administration’s Veterinary Medicine Advisory Committee from 2004 to 2008. In addition, he has provided his biosafety expertise for projects involving the International Food Policy Research Institute, the World Bank, and the Biosafety Project of the UN Environment Programme–Global Environment Facility. Mr. Jaffe earned his B.A. with high honors in biology and government from Wesleyan University and then received a law degree from Harvard Law School.

Dr. Mark D. Needham is a professor in the Department of Forest Ecosystems and Society at Oregon State University (OSU); an adjunct professor in the College of Earth, Ocean, and Atmospheric Sciences at OSU; and an adjunct and affiliate professor in the Department of Geography at the University of Hawaii. He is a social scientist who focuses on understanding human experiences and behavior within the context of nature and uses this to inform land management and advance scientific thought. Dr. Needham's most recent work on forest-related issues includes studies of public attitudes toward using biotechnological (e.g., genetic modification) and nonbiotechnological (e.g., tree breeding, assisted migration) interventions to address forest health threats (e.g., diseases such as chestnut blight, pests such as pine beetle, climate change). He is also working on a study of public trade-offs of ecosystem services associated with aerial herbicide spraying and other intensive management practices on private forestlands. He is editor-in-chief of the international journal *Human Dimensions of Wildlife* and director of the Natural Resources, Tourism, and Recreation (NATURE) Studies Lab at OSU. Dr. Needham received the Academy of Leisure Sciences Excellence in Teaching Award for 2016, Department of Forest Ecosystems and Society Graduate Students' Award for Outstanding Faculty for 2013, College of Forestry Dean's Award for Outstanding Teaching and Advising Professor for 2009, and the College of Forestry Dean's Award for Outstanding Research Professor for 2007. He received his B.A. and M.A. in geography and environmental studies from the University of Victoria in Canada and his Ph.D. in human dimensions of natural resources from Colorado State University.

Dr. Clare Palmer is a professor of philosophy and a Cornerstone faculty fellow in the Liberal Arts at Texas A&M University. She was awarded a B.A. (First Class) with honors from Trinity College, Oxford, and a D.Phil. from Queen's College, Oxford, and has since held academic positions at universities in the United Kingdom, Australia, and the United States. Her primary areas of research are environmental ethics, animal ethics, and the ethics of emerging technologies, in particular, ethical questions raised by the use of biotechnology for conservation goals. She held the elected position of president of the International Society for Environmental Ethics from 2007 to 2010 and currently serves on the editorial boards of interdisciplinary journals, including *Environmental Values*, the *Journal of Agricultural and Environmental Ethics*, *People and Nature*, and *Environmental Humanities*. She is the author or co-author of four books, including *Animal Ethics in Context* (Columbia University Press, 2010) and has edited or co-edited seven other volumes, including, in 2014, *Linking Ecology and Ethics for a Changing World*, a collaboration between philosophers and ecologists. She has more than 100 other publications. She was the founding editor of the journal *Worldviews: Environment, Culture, Religion* (Brill Academic Press), and was co-principal investigator on the National Science Foundation-funded project Genomics and Society from 2012 to 2016.

Dr. Jeanne Romero-Severson is a professor of quantitative genetics and genomics at the University of Notre Dame. She studies population genetics and genomics of adaptive variation for stress resistance in temperate forest trees and insects, including insect vectors of human disease. In her first career in the private sector, she identified genetic determinants of regenerative capacity from tissue culture, resistance to two major potyviruses, and resistance to European corn borer in maize. She led the final effort to produce agronomically acceptable maize inbreds from the first successful *Bt* transformant in maize. In her academic career, she has contributed to the whole-genome sequencing projects for the jewel wasp, a parasite of flies, and the human body louse. Her specialization in statistical genetics and genetic mapping in nonmodel organisms led to the identification of genetic determinants for saltwater tolerance in sibling species of *Anopheles* (malaria vector) mosquitoes. Her group generated the first genetic map for northern red oak, identified the extent of natural hybridization between the native nut tree, butternut, with Japanese heartnut, identified genetically unique populations of butternut in Atlantic Canada, discovered that the rate of regeneration in northern red oak influences estimates of population differentiation, and generated full-sib resource populations for black walnut and northern red oak. Dr. Romero-Severson is currently working on identifying genetic determinants of emerald ash borer resistance in green ash and the functional genomics of multifactor artemisinin resistance in the malaria parasite. She is a member of the governing board of the American Chestnut Foundation, the governing board of the Northern Nut Growers Association, and the advisory group for the Center for Tree Science at the Morton Arboretum. She is also a member of the American

Society of Plant Biologists, the Society of American Foresters, and the American Association for the Advancement of Science. Dr. Romero-Severson is the author or co-author of more than 78 refereed publications. She holds two issued patents and one provisional patent involving plant breeding and analytical chemistry. She received her B.S. in molecular biology and Ph.D. in plant breeding and plant genetics from the University of Wisconsin–Madison.

Dr. Ronald R. Sederoff (NAS) was a distinguished university professor of forestry, Edwin F. Conger Professor of Forestry and Environmental Resources, and co-director of the Forest Biotechnology Group at North Carolina State University. After a stint as a U.S. Forest Service scientist in California, he joined NC State's forestry and environmental resources department in 1987. Dr. Sederoff, one of the first scientists to study molecular genetics of forest trees, established the Forest Biotechnology Group at NC State in 1988. His work focuses on gaining a better understanding of forest tree biology and using that knowledge to accelerate tree breeding. In 1995, Dr. Sederoff was elected to the National Academy of Sciences. He is also a fellow of the American Association for the Advancement of Science and a member of the International Academy of Wood Science. In 2004, he received an honorary doctorate in forest science from the Swedish Agricultural University. He was named the Institute of Forest Biotechnology's 2011 Forest Biotechnologist of the Year, and in 2017 he was awarded the Marcus Wallenberg Foundation Prize, an international award for scientific achievements in fields important to forestry. He received his B.S. in zoology and M.S. and Ph.D. in zoology genetics from the University of California, Los Angeles.

Dr. Diana L. Six is a professor of forest entomology/pathology in the Department of Ecosystem and Conservation Sciences in the W.A. Franke College of Forestry and Conservation at the University of Montana. Her primary research focuses on the evolution and maintenance of symbioses, particularly those occurring among bark beetles, ambrosia beetles, and fungi. This work includes collaborative efforts with scientists in the United States, South Africa, Sweden, and Mexico. Dr. Six also conducts research on various aspects of bark beetle ecology and management, including investigations into how bark beetles may affect the ability of forests to adapt to climate change. She is an associate editor for the journals *Insects*, *Journal of Economic Entomology*, and *Agricultural and Forest Entomology*. Dr. Six is a member of several scientific societies including the Entomological Society of America and the International Symbiosis Society. She received her B.S. in agricultural biology from California State Polytechnic University and M.S. and Ph.D. in entomology from the University of California, Riverside.

Dr. Richard A. Snieszko has worked in forest genetics and tree improvement since 1977. Since 1991, he has been Center Geneticist with the U.S. Department of Agriculture's Forest Service, Pacific Northwest Region's Dorena Genetic Resource Center in Cottage Grove, Oregon. His work focuses on development of genetic resistance to nonnative forest tree diseases as well as genetic variation and genetic conservation in forest trees. His Bachelor of Science degree in forest science is from Humboldt State University, and his Ph.D. in forest genetics is from North Carolina State University. Prior to joining the Forest Service in 1991, he worked in Zimbabwe (3 years) and at Oregon State University (in conjunction with Pacific Northwest Research Station). He is coordinator of International Union of Forest Research Organizations (IUFRO) 2.02.15 Working Group (breeding and genetic resources of five-needle pines) and a member of the IUFRO Task Force on Biological Invasions in Forests. Dr. Snieszko is also initiator and ad hoc coordinator/facilitator for the Genetics of Host–Parasite Interactions in Forestry working group that met in 2011 and 2015 and is scheduled to meet August 5–10, 2018. He oversees programs that have developed genetic resistance to the nonnative pathogens *Cronartium ribicola* and *Phytophthora lateralis* has been technical adviser to the program to develop resistance to koa wilt (caused by *Fusarium oxysporum*) in Hawaii, and has recently started a program in conjunction with Oregon State University to look for resistance to sudden oak death (caused by *P. ramorum*) in tanoak. The programs he oversees are world leaders in the applied development of resistance for reforestation and restoration, and the products from these programs are now used widely across the Pacific Northwest. Since 2001, Dr. Snieszko has organized or co-organized eight international conferences and workshops on genetic resistance, genetic conservation, and white pine genetics/breeding.

He has been principal investigator (PI), co-PI, or cooperator on numerous funded grant proposals, has published numerous papers, and has been an invited speaker on the development and application of disease resistance in forest trees.

Appendix B

Open Session Meeting Agendas

Information-gathering sessions include in-person public meetings and webinars held by the committee from December 2017 to April 2018. They are listed in chronological order. The locations of in-person meetings are provided. Presentations that were made via the Internet at the in-person public meetings are noted.

DECEMBER 1, 2017—FIRST PUBLIC MEETING

The first in-person public meeting of the Committee on the Potential for Biotechnology to Address Forest Health was held at the National Academy of Sciences building in Washington, DC.

Open Session Agenda

December 1, 2017

10:30 a.m.–6:00 p.m.

- | | |
|------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 10:30 a.m. | Welcome and Introductions
Susan Offutt, <i>Committee Chair, National Academies of Sciences, Engineering, and Medicine</i>

Kara Laney, <i>Study Director, National Academies of Sciences, Engineering, and Medicine</i> |
| 10:45 a.m. | U.S. Endowment for Forestry and Communities
Michael Goergen, <i>Vice President, Innovation, and Director, P³Nano</i> |
| 11:10 a.m. | U.S. Department of Agriculture’s Forest Service
Carlos Rodriguez Franco, <i>Deputy Chief</i> |
| 11:35 a.m. | U.S. Department of Agriculture’s Animal and Plant Health Inspection Service
Susan Koehler, <i>Intergovernmental Agricultural Biotechnology Liaison</i> |
| 12:00 p.m. | U.S. Environmental Protection Agency
John Kough, <i>Senior Scientist, Office of Pesticide Programs, Biopesticides and Pollution Prevention Division</i> |
| 12:25 p.m. | Lunch |
| 1:30 p.m. | U.S. Department of Agriculture’s Agricultural Research Service
Kevin Hackett, <i>Senior National Program Leader, Crop Entomology</i> |
| 1:55 p.m. | U.S. Department of Agriculture’s National Institute of Food and Agriculture
Timothy Conner, <i>Director, Division of Bioenergy</i> |

- 2:20 p.m. **General Committee Discussion with Sponsors**
- 2:45 p.m. **Break**
- 3:00 p.m. **Public attitudes and Philosophical Perspectives on the Use of Biotechnology to Address Forest Health**
Evelyn Brister, *Associate Professor, Rochester Institute of Technology*
- 3:30 p.m. **Why Biotech Solutions Are Needed to Address Forest Health**
Steve Strauss, *Professor, Oregon State University*
- 4:00 p.m. **Threats to and Efforts to Protect *Acacia koa* in Hawaii**
Dulal Borthakur, *Professor, University of Hawai'i at Mānoa*
- 4:30 p.m. **How a Single Gene May Help Save the American Chestnut**
William A. Powell, *Professor, SUNY College of Environmental Science and Forestry*
- 5:00 p.m. **General Committee Discussion with Speakers**
- 5:30 p.m. **Public Comment Period**
- 6:00 p.m. **Adjourn Open Session**

DECEMBER 12, 2017—WEBINAR

Tree Breeding for Forest Health—Current Successes. How Can Biotechnology Help?
Richard Sniezko, *U.S. Forest Service*

Emerald Ash Borer—The Complexities of a Catastrophic Invader
Deb McCullough, *Michigan State University*

Developing Genetically Diverse, Blight-Resistant American Chestnut Through Conventional Breeding and Genetic Engineering
Jared Westbrook, *The American Chestnut Foundation*

FEBRUARY 8, 2018—SECOND PUBLIC MEETING

The second in-person public meeting of the Committee on the Potential for Biotechnology to Address Forest Health was held at the National Academy of Sciences building in Washington, DC.

Open Session Agenda
February 8, 2018
10:15 a.m.–3:15 p.m.

- 10:15 a.m. **Welcome and Introductions**
Susan Offutt, *Committee Chair, National Academies of Sciences, Engineering, and Medicine*
- Kara Laney, *Study Director, National Academies of Sciences, Engineering, and Medicine*

Forest Health and Biotechnology: Possibilities and Considerations

- 10:30 a.m. Kimberly F. Wallin, *Research Associate Professor and Interim Associate Dean for Research and Graduate Programs, University of Vermont*
- 10:50 a.m. James S. Clark, *Nicholas Professor in Global Environmental Change and Professor of Statistical Science, Duke University*
- 11:10 a.m. Gary M. Lovett (presenting remotely), *Senior Scientist and Forest Ecologist, Cary Institute of Ecosystem Studies*
- 11:30 a.m. **Discussion with Morning Session Speakers**
- 12:15 p.m. **Lunch**
- 1:00 p.m. Robert L. Deal (presenting remotely), *Research Forester and Ecosystem Services Team Leader, USDA–Forest Service*
- 1:20 p.m. Robert J. Johnston, *Professor of Economics and Director of George Perkins Marsh Institute, Clark University*
- 1:40 p.m. Christine Dean, *Vice President, Global Timberlands Technology (retired), Weyerhaeuser*
Anna Leon, *Forest Pathologist, Weyerhaeuser*
- 2:00 p.m. **Discussion with Afternoon Session Speakers**
- 2:45 p.m. **Public Comment Period**
- 3:15 p.m. **Adjourn Open Session**

FEBRUARY 12, 2018—WEBINAR

Using Genomic Tools to Understand and Manage Adaptation to Climate

Sally Aitken, *University of British Columbia*

FEBRUARY 22, 2018—WEBINAR ON POPLAR AND ASH

Jennifer Koch, *U.S. Forest Service, Northern Research Station*

Jared M. LeBoldus, *Oregon State University*

FEBRUARY 23, 2018—WEBINAR ON PESTICIDE USE IN FORESTS

John L. Kough, *Office of Pesticide Programs, Biopesticides and Pollution Prevention Division, Environmental Protection Agency*

Robyn Rose, *USDA-APHIS, Plant Protection and Quarantine*

**MARCH 2, 2018—WEBINAR ON INDIGENOUS PERSPECTIVES
ON THE USE OF BIOTECHNOLOGY IN FORESTS**

Neil Patterson, *Center for Native Peoples and the Environment, SUNY College of Environmental Science and Forestry*

B.J. McManama, *Indigenous Environmental Network*

Michael J. Dockry, *U.S. Forest Service and University of Minnesota*

MARCH 5, 2018—FOREST ECOLOGY AT THE U.S. FISH & WILDLIFE SERVICE

William C. (Chuck) Hunter, *U.S. Fish & Wildlife Service*

Marit Alanen, *U.S. Fish and Wildlife Service*

MARCH 8, 2018—GE TREES AND THE U.S. REGULATORY SYSTEM

Adam Costanza, *Institute of Forest Biosciences*

Lori Knowles, *University of Alberta and Institute of Forest Biosciences*

William (Bill) Doley, *USDA-APHIS–Biotechnology Regulatory Services*

MARCH 8, 2018—ETHICS OF USING BIOTECHNOLOGY IN CONSERVATION

Ron Sandler, *Northeastern University*

Faith T. Campbell, *Center for Invasive Species Prevention*

**MARCH 27, 2018—RISKS, CONCERNS, AND POTENTIAL PROBLEMS
REGARDING THE USE OF BIOTECHNOLOGY TO ADDRESS FOREST HEALTH**

Rachel Smolker, *BiofuelWatch*

Anne Petermann, *Global Justice Ecology Project*

Ruddy Turnstone, *Global Justice Ecology Project*

MARCH 27, 2018—WHITEBARK PINE

Diana F. Tomback, *University of Colorado Denver*

APRIL 5, 2018—THIRD PUBLIC MEETING

The third in-person public meeting of the Committee on the Potential for Biotechnology to Address Forest Health was held at the National Academy of Sciences building in Washington, DC.

Open Session Agenda

April 5, 2018

10:30 a.m.–3:00 p.m.

10:30 a.m. **Welcome and Introductions**

Susan Offutt, *Committee Chair, National Academies of Sciences, Engineering, and Medicine*

Kara Laney, *Study Director, National Academies of Sciences, Engineering, and Medicine*

- 10:50 a.m. **Risk Assessment to Support Decision Making**
Katherine von Stackelberg, *Research Scientist, Center for Health and the Global Environment and the Harvard Center for Risk Analysis*
- 11:10 a.m. **Importance of Incorporating Ecosystem Services Within the Context of Social-Ecological Systems**
Lawrence Kapustka, *Senior Ecologist, LK Consultancy*
- 11:30 a.m. **Discussion with Morning Session Speakers**
- 12:00 p.m. **Lunch**
- 1:00 p.m. **Improved Assessment of Risks of Gene Flow in the Environment**
Nathalie Isabel, *Research Scientist, Canadian Forest Service*
- 1:20 p.m. **Levels and Logics of Public and Stakeholder Support for the Use of Genomic Tools for Forest Adaptation**
Shannon Hagerman, *Assistant Professor of Social-Ecological Systems, University of British Columbia*
- 1:40 p.m. **Discussion with All Speakers**
- 2:45 p.m. **Public Comment Period**
- 3:00 p.m. **Adjourn Open Session**

Appendix C

Biotech Tree Research and Development, 1987–2018

Species	Common Name	Hybrid of?	Insect/Fungus/Pest/Other Trait	Common Name/Taxonomy	Biotech Approach	Targeted Genes/Other	Final Outcome	Country of Report	Reference
Poplars									
<i>Populus tomentosa</i>	Chinese white poplar		<i>Clostera anachoreta</i>	Moth	Transformation	<i>Cry1Ac</i>	Resistance in field trial	China	Ren et al., 2018
			<i>Lymantria dispar</i>	Gypsy moth	Transformation		Resistance in field trial	China	Ren et al., 2018
<i>Populus</i> sp. hybrid	741 clone Poplar	<i>Populus alba</i> L. × (<i>P. davidiana</i> Dode + <i>P. simonii</i> Carr.) × <i>P. tomentosa</i> Carr.		Lepidopterans	Transformation	<i>Cry1Ac</i> , <i>Cry3A</i> , <i>np1II</i>	Resistance	China	Zuo et al., 2018
<i>Populus</i> sp.	Hybrid poplar	<i>P. alba</i> × <i>P. grandidentata</i>	<i>Melampsora aecidiodes</i>	Leaf rust fungus	Transformation	<i>AtGolS3</i> (<i>A. thaliana</i>)	Repressed resistance to leaf rust & enhanced ROS tolerance	Canada	La Mantia et al., 2018
<i>Populus</i> sp.	Hybrid poplar	<i>P. alba</i> × <i>P. grandidentata</i>	<i>Melampsora aecidiodes</i>	Leaf rust fungus	Transformation	<i>CsRFS</i> (<i>Cucumis sativus</i>)	Repressed resistance to leaf rust & enhanced ROS tolerance	Canada	La Mantia et al., 2018
<i>Populus</i> sp.	84K poplar	<i>P. alba</i> × <i>P. glandulosa</i>	Drought tolerance		Transformation	<i>PeCHYR1</i> (from <i>P. euphratica</i>)	Increased WUE and drought tolerance	China	He et al., 2018
<i>Salix mongolica</i>					Transformation—proof of concept	GUS	Proof of concept transformation	China	Guan et al., 2018
<i>Populus</i> sp.	Haploid poplar	<i>P. simonii</i> × <i>P. nigra</i>	Early flowering		Transformation with gene from <i>Salix integra</i>	<i>API</i> (Apetala 1)	Early flowering transgenics	China	Yang et al., 2018
<i>Populus tomentosa</i>	Poplar		<i>Melampsora</i> sp.	Leaf rust fungus	Transformation	<i>PtWRKY18</i> & <i>PtWRKY35</i>	resistance to <i>Melampsora</i> fungus	China	Jiang et al., 2017
<i>Populus</i> sp. hybrid	Hybrid poplar	<i>P. alba</i> × <i>P. tremula</i> 717 clone	Mechanism of lignin biosynthesis		CRISPR/Cas9	<i>4CL1</i> , <i>4CL2</i>	Downregulation of genes through CRISPR mutagenesis	USA	Zhou et al., 2015
<i>Populus tomentosa</i>	Poplar		gGene knockout		CRISPR/Cas9	<i>PtoPDS</i>	Gene knocked out	China	Fan et al., 2015

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Poplars									
<i>Populus</i> sp.	Hybrid poplar	<i>P. alba</i> × <i>P. tremula</i> var <i>glandulosa</i>	Enhanced wood production		Transformation with gene from <i>Pinus densiflora</i>	Gibberellin 20-oxidase 1	Enhanced wood production with gelatinous wood fibers	Republic of Korea, Canada	Park et al., 2015
<i>Populus</i> sp.	Poplars	<i>P. tremula</i> × <i>P. alba</i> var <i>glandula</i>	Heavy metal remediation		Transformation	<i>ScYCF1</i>	Heavy cadmium tolerance	Republic of Korea	Shim et al., 2013
<i>Populus tomentosa</i>	Chinese white poplar		<i>Alternaria alternata</i>	Poplar leaf blight	Transformation	<i>Bbchit1</i> & <i>LJAMP2</i>	Resistance to both diseases	China	Huang et al., 2012
			<i>Colletotrichum</i> sp.	Anthracnose disease	Transformation	<i>Bbchit1</i> & <i>LJAMP2</i>		China	Huang et al., 2012
<i>Populus</i> sp.	Hybrid poplar	<i>P. nigra</i> × <i>P. maximowiczii</i>	<i>Melampsora medusae</i>	Leaf rust	Transformation	<i>ech42</i> (endocytinase gene from <i>Trichoderma harzianum</i>)	Resistance to leaf rust	Canada	Noël et al., 2009
<i>Populus</i> sp.			<i>Anoplophora glabripennis</i>	Asian longhorned beetle	Bt886 expression in <i>E. coli</i>	<i>Cry3Aa</i>	Expression of gene is toxic to the beetle in <i>E. coli</i>	China	Chen et al., 2005
<i>Populus</i> sp.	Poplars	[(<i>Populus tomentosa</i> × <i>P. bolleana</i>) × <i>P. tomentosa</i>]	<i>Malacosoma disstria</i> , <i>Lymantria dispar</i> , <i>Stilpnolia candida</i>	Moths	Transformation	<i>CpTI</i> (cowpea trypsin inhibitor)	High resistance to moths	China	Zhang et al., 2004
<i>Populus</i> sp. hybrid	INRA 353-38	<i>P. tremula</i> × <i>P. tremuloides</i>	<i>Chrysomela tremulae</i>	Arthropod	Transformation	<i>Cry3Aa</i>	Resistance	France	Génissel et al., 2003
<i>Populus</i> sp.	Hybrid poplar	<i>P. tremula</i> × <i>P. tremuloides</i>	<i>Chrysomela tremulae</i>	Arthropod	Transformation	<i>Cry3Aa</i>	Resistance	France	Génissel et al., 2003
<i>Populus</i> sp.	Hybrid poplar Ogy	<i>Populus</i> × <i>P. euamericana</i>	<i>Septoria musiva</i>	Leaf spot disease	Transformation	OxO	Resistance to <i>Septoria</i>	USA	Liang et al., 2001
<i>Populus</i> sp.	Hybrid poplar N-106	<i>P. deltoides</i> × <i>P. simonii</i>	<i>Lymantria dispar</i>	Gypsy moth	Transformation	AaIT (scorpion neurotoxin)	Resistance to gypsy moth	China	Wu et al., 2000
Chestnut									
<i>Castanea dentata</i>	American chestnut	with Chinese chestnut	<i>Cryphonectria parasitica</i>	Chestnut blight fungus	Transformation	Oxalate oxidase (wheat)	Resistance against chestnut blight fungus	USA	Newhouse et al., 2014
<i>Castanea dentata</i>	American chestnut		<i>Cryphonectria parasitica</i>	Chestnut blight fungus	Transformation—proof of concept	<i>gfp</i> , <i>bar</i> , OxO	Transformation—proof of concept	USA	Polin et al., 2006
<i>Castanea sativa</i>	European chestnut				Transformation—proof of concept	<i>nptII</i> , <i>uidA</i>	Transformation—proof of concept	Spain	Corredoira et al., 2004

Eucalypts									
<i>Eucalyptus</i> sp.			Realized pollen flow assessment			GM eucalypt	No pollen flow beyond 240 m in a stand that was established in 2009	Brazil	da Silva et al., 2017
<i>Eucalyptus</i> sp.		<i>E. urophylla</i> × <i>E. grandis</i>	<i>Ralstonia solanacearum</i>	Bacterial wilt, fungal infection, gray mold	Transformation	<i>atiA</i>	Bacterial wilt resistance	China	Ouyang and Li, 2016
<i>Eucalyptus globulus</i>			Salt tolerance		Transformation	<i>codA</i>	Salt tolerance and no adverse effect on soil microbial communities in a 4-year trial	Japan	Oguchi et al., 2014
						Mangrin	Increase salt tolerance	Japan, Pakistan	Yu et al., 2013
<i>Eucalyptus camaldulensis</i>	Red river gum		Salt tolerance			<i>codA</i> family	Increase salt tolerance	Japan	Kikuchi et al., 2009
<i>Eucalyptus</i> sp.		<i>E. urophylla</i> × <i>E. grandis</i>	Frost tolerance		Transformation	<i>CBF2 (A. thaliana)</i>	Increase freeze tolerance	USA	Hinchee et al., 2009
Ash									
<i>Fraxinus pennsylvanica</i>	Green ash		Proof-of-concept transformation		Transformation	<i>nptII</i> , GUS		USA	Du and Pijut, 2009
Birch									
<i>Betula platyphylla</i>	Birch		Salt/drought tolerance		Transformation	<i>BpSPL9</i>	Improved ROS scavenging leading to better salt/drought tolerance in transgenic lines	China	Ning et al., 2017
<i>Betula platyphylla</i>	Birch		Salt tolerance		Transformation	BplMYB46	Overexpression induces improved ROS scavenging	China	Guo et al., 2016
<i>Betula platyphylla</i>	Birch		<i>Lymantria dispar</i>	Gypsy moth	Transformation	<i>bgt</i>	Resistance to gypsy moth	China	Zeng et al., 2009
<i>Betula pendula</i>	Silver birch		<i>Pyrenopeziza betulicola</i>	Fuckel leaf spot disease	Transformation	Chitinase 4 (sugar beet)	Resistance to leaf spot disease	Finland	Pappinen et al. 2002
Spruce									
<i>Picea glauca</i>	White spruce		<i>Choristoneura fumiferana</i>	Spruce budworm	Transformation	<i>PBgGlu1</i>	Resistance to budworm	Canada	Mageroy et al., 2017
<i>Picea abies</i>	Norway spruce		<i>Heterobasidion annosum</i>	Annosum root rot	Transformation	<i>PaNACO3</i>	Resistance to fungus	Sweden	Dalman et al., 2017
<i>Picea abies</i>	Norway spruce		<i>Cyatocystis polonica</i>	Bark beetle co-invading fungus	Transformation	Flavan-3-ols, LAR	Resistance to fungus	Canada	Hammerbacher et al., 2014

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Spruce									
<i>Picea glauca</i>	White spruce				Somatic embryogenesis	<i>CHAP3A</i> & WUS		Canada	Klimaszewska et al., 2010
<i>Picea mariana</i>	Black spruce		<i>Cylindrocladium floridanum</i>	Root pathogen	Transformation	<i>ech42</i> (endocitinase gene from <i>Trichoderma harzianum</i>)	Resistance to root disease	Canada	Noël et al., 2009
<i>Picea glauca</i>	White spruce		Functional characterization: CAD		Post-transformation analysis	CAD	Validation of CAD transformation	Canada, France	Bedon et al., 2009
<i>Picea glauca</i>	White spruce		<i>Choristoneura fumiferana</i>	Spruce budworm	Transformation	<i>CryIAB</i>	Resistant to spruce budworm	Canada	Lachance et al., 2007
<i>Picea glauca</i>	White spruce				Transformation to test effect on rhizosphere communities	<i>nptII</i> , <i>CryIA</i> , <i>uidA</i>	Rhizosphere communities significantly affected by transgenes	Canada	LeBlanc et al., 2007
<i>Picea glauca</i>	White spruce				Transformation proof of concept	<i>nptII</i> , <i>uidA</i>		Canada	Le et al., 2001
<i>Picea abies</i>	Norway spruce				Particle bombardment	<i>bar</i>	Resistant to Basta herbicide	Sweden	Brukhin et al., 2000
<i>Picea mariana</i>	Black spruce				Particle bombardment	<i>nptII</i> , GUS	Proof-of-concept transformation	Canada	Charest et al., 1996
Douglas Fir									
<i>Pseudotsuga menziesii</i>	Douglas fir		Proof of concept		Transformation	Kanamycin resistance	Proof-of-concept transformation	USA	Dandekar et al., 1987
<i>Pseudotsuga menziesii</i>	Douglas fir		Proof of concept		Particle bombardment	GUS	Proof of concept	USA	Goldfarb et al., 1991
Larch									
<i>Larix</i> sp.	Larch	<i>L. kaempferi</i> × <i>L. decidua</i>	Proof of concept		Transformation	Kanamycin resistance	Proof-of-concept transformation	France, Canada	Levéé et al., 1997
<i>Larix decidua</i>	European larch		Proof of concept		Transformation		Proof-of-concept transformation	USA	Huang et al., 1991
Pines									
<i>Pinus massoniana</i>	Masson pine				Transformation—proof of concept	<i>CsIA2</i>	Proof-of-concept transformation	China	Maleki et al., 2018
<i>Pinus elliotii</i>	Hybrid pine	<i>P. elliotii</i> var. <i>elliotii</i> × <i>P. caribaea</i> var. <i>hondurensis</i>			Somatic embryogenesis		Proof of concept	Portugal	Nunes et al., 2018

<i>Pinus pinea</i>	Stone pine				Transformation—proof of concept	GUS	Proof-of-concept transformation	Spain, Ecuador	Blasco et al., 2016
<i>Pinus radiata</i>	Radiata pine				Transformation of micropropagated shoots	<i>nptII</i> , GUS	Proof-of-concept transformation	New Zealand	Grant et al., 2015
<i>Pinus thunbergii</i>	Japanese black pine				Somatic embryogenesis		Proof of concept	Japan	Martuyama and Hosoi, 2016
<i>Pinus radiata</i>	Radiata pine		Syringil lignin production		Transformation	F5H, COMT	Syringil lignin production in conifers	USA, New Zealand	Wagner et al., 2015
<i>Pinus elliottii</i>	Slash pine				Transformation—proof of concept	<i>hpt</i> , <i>uidA</i>	Proof-of-concept transformation	China	Tang et al., 2014
<i>Pinus radiata</i>	Radiata pine		Lignin composition changes		RNAi suppression and transformation	CCoA reductase	Changes to cell wall composition	New Zealand, USA, Belgium	Wagner et al., 2013
<i>Pinus radiata</i>	Radiata pine		Lignin reduction		Transformation	<i>PrCCoAOMT</i>	Modification of lignin composition	New Zealand	Wagner et al., 2011
<i>Pinus radiata</i>	Radiata pine				Transformation—proof of concept	<i>nptII</i> , <i>uidA</i> , <i>bar</i>	Proof-of-concept transformation	New Zealand	Charity et al., 2005
<i>Pinus radiata</i>	Radiata pine		Gene silencing		Transformation	CAD	Silencing of CAD gene	New Zealand, Australia	Wagner et al., 2005
<i>Pinus taeda</i>	Loblolly pine		<i>Dendrolimus punctatus</i> & <i>Cryphothoelea formicicola</i>	Moth pests of pines	Transformation	<i>CryIAc</i>	Resistance to moth pests	USA	Tang and Tian, 2003
<i>Pinus strobus</i>	Eastern white pine		Proof of concept		Transformation	GUS	Proof-of-concept transformation	Canada	Levéé et al., 1999
Elm									
<i>Ulmus americana</i>	American elm		<i>Ophiostoma novoulmi</i>	Dutch elm disease	Transformation	<i>ESF39A</i>	Resistance to Dutch elm disease	USA	Newhouse et al., 2007
<i>Ulmus procera</i>	English elm		<i>Ophiostoma novoulmi</i>	Dutch elm disease	Transformation—proof of concept	<i>nptII</i> , <i>uidA</i>	Proof-of-concept transformation	USA	Gartland et al., 2000
Apple									
<i>Malus × domestica</i>	Apple		Dwarf phenotype		Transformation	<i>MdNAC1</i>	Overexpression results in dwarf phenotype	China	Jia et al., 2018
<i>Malus × domestica</i>	Apple		Stress tolerance		Transformation	<i>MdATG18a</i>	Tolerance to drought stress	China, USA	Sun et al., 2018
<i>Malus × domestica</i>	Apple		Stress tolerance		Transformation	<i>MdcyMDH</i>	Tolerance to cold and salt stresses	China	Wang et al., 2016
<i>Malus × domestica</i>	Apple		<i>Venturia inaequalis</i>	Scab	Transformation	Puroindoline-B (<i>pinB</i>)	Reduction in scab susceptibility	France	Faize et al., 2004
<i>Malus × domestica</i>	Apple		Early flowering		Transformation	<i>MdTFL</i>	Early onset of flowering (15 months)	Japan	Kotoda et al., 2002

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Cherry									
<i>Prunus avium</i>	Cherry		Proof-of-concept regeneration		Transformation	<i>gusA</i> , <i>vcFT</i>	Shoot regeneration/proof of concept	USA, China, Egypt	Zong et al., 2018
<i>Prunus</i> sp.	Black cherry		Flowering control & insect resistance	Bark beetles	Transformation	PH3, <i>MDL4</i> , <i>PsTFL1</i>	Early flowering and pest resistance	USA	Wang and Pijut, 2014
<i>Prunus</i> sp.	Cherry	Gisela 6 and Gisela 7	Proof of concept	Necrotic ring spot virus	Transformation	RNAi	Resistance to <i>Prunus</i> necrotic ringspot virus	USA	Song et al., 2013
<i>Prunus serotina</i>	Black cherry		Proof of concept		Transformation	Agamous	Proof-of-concept transformation	USA	Liu and Pijut, 2010
<i>Prunus cerasus</i> & hybrid	Cherry	<i>P. cerasus</i> × <i>P. canescens</i>	Proof of concept		Transformation	<i>nptII</i> , <i>gusA</i>	Proof-of-concept transformation	USA	Song and Sink, 2006
<i>Prunus</i> sp.	Cherry	<i>P. avium</i> × <i>P. pseudocerasus</i>	Proof of concept		Somatic embryogenesis		Proof of concept	Italy	Gutiérrez-Pesce and Rugini, 2004
<i>Prunus</i> sp.	Cherry	<i>P. avium</i> × <i>P. pseudocerasus</i>	Proof of concept		Transformation		Proof of concept	Italy, USA	Gutiérrez-Pesce et al., 1998
Peach									
<i>Prunus persica</i>	Peach		Proof of concept		Transformation	GUS, GFP	Proof of concept transformation	USA, Poland, Italy, Spain	Padilla et al., 2006
<i>Prunus persica</i>	Peach		Proof-of-concept regeneration		Transformation and regeneration	<i>nptII</i> , <i>sGFP</i>	Regeneration of transformed plants	Spain	Pérez-Clemente et al., 2005
Papaya									
<i>Carica papaya</i>	Papaya			Ring spot virus	Transformation	Coat protein gene <i>CP</i>	Resistance to PRSV	China, Taiwan	Bau et al., 2003
<i>Carica papaya</i>	Papaya			Ring spot virus	RNAi particle bombardment	Coat protein gene <i>CP</i>	Resistance to PRSV	China, Taiwan	Jia et al., 2017
Walnut									
<i>Juglans regia</i>	Persian walnut				Transformation	<i>fld</i>	Increased tolerance to osmotic stress	Iran	Sheikh Beig Goharizi et al., 2016
<i>Juglans regia</i>	Walnut				Transformation	<i>nptII</i> , <i>uidA</i>	Proof-of-concept transformation	USA	Walawage et al., 2014
<i>Juglans</i> sp.	Walnut	<i>J. hindsii</i> × <i>J. regia</i>			Transformation	<i>rolABC</i>	Induce rooting in hybrids	USA	Vahdati et al., 2002
<i>Juglans regia</i>	Walnut		<i>Cydia pomonella</i>	Codling moth	<i>Bt</i> transformation	<i>CryIIA(c)</i>	Resistance to insects	USA	Dandekar et al., 1998
<i>Juglans regia</i>	Walnut		Proof of concept		Transformation and regeneration	<i>APHII</i>	Transformation and regeneration of plants	USA	McGranahan et al., 1988

Plum									
<i>Prunus</i> sp.	Plum	(<i>P. pumila</i> × <i>P. salicina</i>) × <i>P. cerasifera</i>	Plum pox virus (PPV)	Plum pox virus	RNAi	PPV-CV	Resistance to PPV	Russia	Sidorova et al., 2018
<i>Prunus</i> sp.	Plum		Plum pox virus (PPV)		Transformation	PPV-CV	Resistance to PPV	France, USA	Scorza et al., 1994
Avocado									
<i>Persea americana</i>	Avocado		Proof of concept		Transformation	<i>gfp</i> , <i>DsRed</i> , <i>gfp-gus</i>	Proof-of-concept transformation and plant recovery	Spain	Palomo-Rios et al., 2017
Black Locust									
<i>Robinia pseudoacacia</i>	Black locust		Proof of concept		Transformation	Kanamycin-resistant gene	Proof-of-concept transformation	USA	Han et al., 1993
<i>Robinia pseudoacacia</i>	Black locust		Herbicide tolerance		Transformation with sonication	<i>bar</i> , <i>gusA</i>	Herbicide tolerance	Spain	Zaragoza et al., 2004
<i>Robinia pseudoacacia</i>	Black locust		Proof of concept		Transformation	GUS	Proof-of-concept transformation	Japan	Igasaki et al., 2000
<i>Robinia pseudoacacia</i>	Black locust		Proof of concept		Transformation	<i>nptII</i> , GUS	Proof-of-concept transformation	India	Kanwar et al., 2003
Citrus									
<i>Citrus</i> sp.	Citrus	(<i>C. sinensis</i> & <i>C. paradisi</i>) × <i>Poncirus trifoliata</i>	Proof of concept		Transformation	<i>nptII</i> , GUS	Proof of concept	Brazil, USA	de Oliveira et al., 2009
<i>Citrus jambhiri</i>	Rough lemon		Proof of concept		Transformation (protoplasts)	<i>nptII</i> & <i>cat</i>	Proof of concept	Israel	Vardi et al., 1990
<i>Citrus sinensis</i>	Citrus		Disease resistance	<i>Xanthomonas axonopodis</i>	Transformation	<i>hrpN</i>	Resistance to citrus canker	Brazil, USA	Barbosa-Mendes et al., 2009
Sweetgum									
<i>Liquidambar styraciflua</i>			Proof of concept		Transformation	Kanamycin & GUS	Proof of concept	USA	Sullivan and Lagrimini, 1993
<i>Liquidambar formosana</i>	Chinese sweetgum		Stress tolerance		Transformation	<i>AtNHXI</i>	Tolerance to salt stress	China	Qiao et al., 2010
<i>Liquidambar</i> sp.	Hybrid Sweetgum	<i>L. styraciflua</i> × <i>L. formosana</i>	Phytoremediation		Transformation	<i>ECS</i> & <i>merA</i>	Mercury phytoremediation	USA	Dai et al., 2009
<i>Liquidambar styraciflua</i>			Insect resistance	<i>Lymantria dispar</i>	Transformation	Tobacco anionic peroxidase	Gypsy moth resistance	USA	Dowd et al., 1998
<i>Liquidambar formosana</i>	Chinese sweetgum		Stress tolerance		Transformation	<i>SOD</i> & <i>POD</i>	Tolerance to salt, drought, and cold	China	Renying et al., 2007

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Cocoa									
<i>Theobroma cocoa</i>	Cocoa		Proof of concept		Transformation	Kanamycin & <i>nptII</i>	Proof of concept	USA, Ghana	Sain et al., 1994
<i>Theobroma cocoa</i>	Cocoa		Proof of concept		Transformation	<i>uidA</i>	Proof of concept	Brazil	Silva et al., 2009
<i>Theobroma cocoa</i>	Cocoa		Proof of concept		Transformation	<i>Chi</i> , <i>nptII</i> , & <i>EGFP</i>	Proof of concept	USA	Maximova et al., 2003
<i>Theobroma cocoa</i>	Cocoa		Fungal resistance	<i>Colletotrichum gloeosporoides</i>	Transformation	<i>TcChi1</i>	Resistance to <i>Colletotrichum</i>	USA	Maximova et al., 2006
<i>Theobroma cocoa</i>	Cocoa		Proof of concept		Somatic embryogenesis		Proof of concept	Colombia	Ramirez et al., 2018
<i>Theobroma cocoa</i>	Cocoa		Proof of concept		Transformation	GFP	Proof of concept	USA	Fister et al., 2016

REFERENCES

- Barbosa-Mendes, J.M., F.D.A. Mourao Filho, A. Bergamin Filho, R. Harakava, S.V. Beer, and B.M.J. Mendes. 2009. Genetic transformation of *Citrus sinensis* cv. Hamlin with *hrpN* gene from *Erwinia amylovora* and evaluation of the transgenic lines for resistance to citrus canker. *Scientia Horticulturae* 122(1):109–115.
- Bau, H.J., Y.H. Cheng, T.A. Yu, J.S. Yang, and S.D. Yeh. 2003. Broad-spectrum resistance to different geographic strains of Papaya ringspot virus in coat protein gene transgenic papaya. *Phytopathology* 93(1):112–120.
- Bedon, F., C. Levasseur, J. Grima-Pettenati, A. Séguin, and J. MacKay. 2009. Sequence analysis and functional characterization of the promoter of the *Picea glauca* cinnamyl alcohol dehydrogenase gene in transgenic white spruce plants. *Plant Cell Reports* 28(5):787–800.
- Blasco, M., J. Muñoz-Bertomeu, J. Segura, and I. Arrillaga. 2016. Optimizing DNA delivery into stone pine embryonic lines. *JSM Genetics & Genomics* 3(3):1020.
- Brukhin, V., D. Clapham, M. Elfstrand, and S. Von Arnold. 2000. Basta tolerance as a selectable and screening marker for transgenic plants of Norway spruce. *Plant Cell Reports* 19(9):899–903.
- Charest, P.J., Y. Devantier, and D. Lachance. 1996. Stable genetic transformation of *Picea mariana* (black spruce) via particle bombardment. *In Vitro—Plant* 32(2):91–99.
- Charity, J.A., L. Holland, L.J. Grace, and C. Walter. 2005. Consistent and stable expression of the *nptII*, *uidA* and *bar* genes in transgenic *Pinus radiata* after *Agrobacterium tumefaciens*-mediated transformation using nurse cultures. *Plant Cell Reports* 23(9):606–616.
- Chen, J., L.Y. Dai, X.P. Wang, Y.C. Tian, and M.Z. Lu. 2005. The *cry3Aa* gene of *Bacillus thuringiensis* Bt886 encodes a toxin against long-horned beetles. *Applied Microbiology and Biotechnology* 67(3):351–356.
- Corredoira, E., D. Montenegro, M.C. San-José, A.M. Vieitez, and A. Ballester. 2004. *Agrobacterium*-mediated transformation of European chestnut embryogenic cultures. *Plant Cell Reports* 23:311–318.
- da Silva, P.H., A.M. Sebbenn, D. Grattapaglia, and J.L.F. Conti, Jr. 2017. Realized pollen flow and wildling establishment from a genetically modified eucalypt field trial in southeastern Brazil. *Forest Ecology and Management* 385:161–166.
- Dai, J., R. Balish, R.B. Meagher, and S. Merkle. 2009. Development of transgenic hybrid sweetgum (*Liquidambar styraciflua* × *L. formosana*) expressing γ -glutamylcysteine synthetase or mercuric reductase for phytoremediation of mercury pollution. *New Forests* 38(1):35–52.
- Dalman, K., J.J. Wind, M. Nemesio-Gorritz, A. Hammerbacher, K. Lundén, I. Ezcurra, and M. Elfstrand. 2017. Overexpression of *PaNAC03*, a stress induced NAC gene family transcription factor in Norway spruce leads to reduced flavonol biosynthesis and aberrant embryo development. *BMC Plant Biology* 17(1):6.
- Dandekar, A.M., P.K. Gupta, D.J. Durzan, and V. Knauf. 1987. Transformation and foreign gene expression in micropropagated douglas-fir (*Pseudotsuga menziesii*). *Nature Biotechnology* 5(6):587–590.
- Dandekar, A.M., G.H. McGranahan, P.V. Vail, S.L. Uratsu, C.A. Leslie, and J.S. Tebbets. 1998. High levels of expression of full-length *cryIA(c)* gene from *Bacillus thuringiensis* in transgenic somatic walnut embryos. *Plant Science* 131(2):181–193.
- de Oliveira, M.L.P., V.J. Febres, M.G.C. Costa, G.A. Moore, and W.C. Otoni. 2009. High-efficiency *Agrobacterium*-mediated transformation of citrus via sonication and vacuum infiltration. *Plant Cell Reports* 28(3):387.
- Dowd, P.F., L.M. Lagrimini, and D.A. Herms. 1998. Differential leaf resistance to insects of transgenic sweetgum (*Liquidambar styraciflua*) expressing tobacco anionic peroxidase. *Cellular and Molecular Life Sciences* 54(7):712–720.
- Du, N., and P.M. Pijut. 2009. *Agrobacterium*-mediated transformation of *Fraxinus pennsylvanica* hypocotyls and plant regeneration. *Plant Cell Reports* 28(6):915–923.
- Faize, M., S. Sourice, F. Dupuis, L. Parisi, M.F. Gautier, and E. Chevreau. 2004. Expression of wheat puroindoline-b reduces scab susceptibility in transgenic apple (*Malus* × *domestica* Borkh.). *Plant Science* 167(2):347–354.
- Fan, D., T. Liu, C. Li, B. Jiao, S. Li, Y. Hou, and K. Luo. 2015. Efficient CRISPR/Cas9-mediated targeted mutagenesis in *Populus* in the first generation. *Scientific Reports* 5:12217.
- Fister, A.S., Z. Shi, Y. Zhang, E.E. Helliwell, S.N. Maximova, and M.J. Gultinan. 2016. Protocol: Transient expression system for functional genomics in the tropical tree *Theobroma cacao* L. *Plant Methods* 12(1):19.
- Gartland, J.S., A.T. McHugh, C.M. Brasier, R.J. Irvine, T.M. Fenning, and K.M. Gartland. 2000. Regeneration of phenotypically normal English elm (*Ulmus procera*) plantlets following transformation with an *Agrobacterium tumefaciens* binary vector. *Tree Physiology* 20(13):901–907.
- Génissel, A., J.C. Leplé, N. Millet, S. Augustin, L. Jouanin, and G. Pilate. 2003. High tolerance against *Chrysomela tremulae* of transgenic poplar plants expressing a synthetic *cry3Aa* gene from *Bacillus thuringiensis* ssp *tenebrionis*. *Molecular Breeding* 11(2):103–110.

- Goldfarb, B., S.H. Strauss, G.T. Howe, and J.B. Zaerr. 1991. Transient gene expression of microprojectile-introduced DNA in Douglas-fir cotyledons. *Plant Cell Reports* 10(10):517–521.
- Grant, J.E., P.A. Cooper, and T.M. Dale. 2015. Genetic transformation of micropropagated shoots of *Pinus radiata* D. Don. *bioRxiv* 030080.
- Guan, Q., M. He, H. Ma, X. Liao, Z. Wang, and S. Liu. 2018. Construction of genetic transformation system of *Salix mongolica*: In vitro leaf-based callus induction, adventitious buds differentiation, and plant regeneration. *Plant Cell, Tissue and Organ Culture* 132(1):213–217.
- Guo, H., Y. Wang, L. Wang, P. Hu, Y. Wang, Y. Jia, C. Zhang, Y. Zhang, Y. Zhang, C. Wang, and C. Yang. 2017. Expression of the MYB transcription factor gene *BpMYB46* affects abiotic stress tolerance and secondary cell wall deposition in *Betula platyphylla*. *Plant Biotechnology Journal* 15(1):107–121.
- Gutiérrez-Pesce, P.G., and E. Rugini. 2004. Influence of plant growth regulators, carbon sources and iron on the cyclic secondary somatic embryogenesis and plant regeneration of transgenic cherry rootstock “Colt” (*Prunus avium* × *P. pseudocerasus*). *Plant Cell, Tissue and Organ Culture* 79(2):223–232.
- Gutiérrez-Pesce, P., K. Taylor, R. Muleo, and E. Rugini. 1998. Somatic embryogenesis and shoot regeneration from transgenic roots of the cherry rootstock Colt (*Prunus avium* × *P. pseudocerasus*) mediated by pRi 1855 T-DNA of *Agrobacterium rhizogenes*. *Plant Cell Reports* 17(6–7):574–580.
- Hammerbacher, A., C. Paetz, L.P. Wright, T.C. Fischer, J. Bohlmann, A.J. Davis, T.M. Fenning, J. Gershenzon, and A. Schmidt. 2014. Flavan-3-ols in Norway spruce: Biosynthesis, accumulation, and function in response to attack by the bark beetle-associated fungus *Ceratocystis polonica*. *Plant Physiology* 164(4):2107–2122.
- Han, K.H., D.E. Keathley, J.M. Davis, and M.P. Gordon. 1993. Regeneration of a transgenic woody legume (*Robinia pseudoacacia* L., black locust) and morphological alterations induced by *Agrobacterium rhizogenes*-mediated transformation. *Plant Science* 88(2):149–157.
- He, F., H.L. Wang, H.G. Li, Y. Su, S. Li, Y. Yang, C.H. Feng, W. Yin, and X. Xia. 2018. Pe CHYR 1, a ubiquitin E3 ligase from *Populus euphratica*, enhances drought tolerance via ABA induced stomatal closure by ROS production in *Populus*. *Plant Biotechnology Journal* 16(8): 1514–1528.
- Hinchee, M., W. Rottmann, L. Mullinax, C. Zhang, S. Chang, M. Cunningham, L. Pearson, and N. Nehra. 2009. Short-rotation woody crops for bioenergy and biofuels applications. *In Vitro Cellular & Developmental Biology* 45(6):619–629.
- Huang, Y., A.M. Diner, and D.F. Karnosky. 1991. *Agrobacterium rhizogenes*-mediated genetic transformation and regeneration of a conifer: *Larix decidua*. *In Vitro Cellular & Developmental Biology—Plant* 27(4):201–207.
- Huang, Y., H. Liu, Z. Jia, Q. Fang, and K. Luo. 2012. Combined expression of antimicrobial genes (*Bbchit1* and *LJAMP2*) in transgenic poplar enhances resistance to fungal pathogens. *Tree Physiology* 32(10):1313–1320.
- Igasaki, T., T. Mohri, H. Ichikawa, and K. Shinohara. 2000. *Agrobacterium tumefaciens*-mediated transformation of *Robinia pseudoacacia*. *Plant Cell Reports* 19(5):448–453.
- Jia, D., X. Gong, M. Li, C. Li, T. Sun, and F. Ma. 2018. Overexpression of a novel apple NAC transcription factor gene, *MdNAC1*, confers the dwarf phenotype in transgenic apple (*Malus domestica*). *Genes* 9(5):229–246.
- Jia, R., H. Zhao, J. Huang, H. Kong, Y. Zhang, J. Guo, Q. Huang, Y. Guo, Q. Wei, J. Zuo, and Y.J. Zhu. 2017. Use of RNAi technology to develop a PRSV-resistant transgenic papaya. *Scientific Reports* 7(1):12636.
- Jiang, Y., L. Guo, X. Ma, X. Zhao, B. Jiao, C. Li, and K. Luo. 2017. The WRKY transcription factors PtrWRKY18 and PtrWRKY35 promote *Melampsora* resistance in *Populus*. *Tree Physiology* 37(5):665–675.
- Kanwar, K., A. Bhardwaj, S. Agarwal, and D.R. Sharma. 2003. Genetic transformation of *Robinia pseudoacacia* by *Agrobacterium tumefaciens*. *Indian Journal of Experimental Biology* 41:149–153.
- Kikuchi, A., X. Yu, T. Shimazaki, A. Kawaoka, H. Ebinuma, and K.N. Watanabe. 2009. Allelopathy assessments for the environmental biosafety of the salt-tolerant transgenic *Eucalyptus camaldulensis*, genotypes *codA12-5B*, *codA12-5C*, and *codA20C*. *Journal of Wood Science* 55(2):149–153.
- Klimaszewska, K., G. Pelletier, C. Overton, D. Stewart, and R.G. Rutledge. 2010. Hormonally regulated overexpression of *Arabidopsis WUS* and conifer *LEC1 (CHAP3A)* in transgenic white spruce: Implications for somatic embryo development and somatic seedling growth. *Plant Cell Reports* 29(7):723–734.
- Kotoda, N., M. Wada, T. Masuda, and J. Soejima. 2002. The break-through in the reduction of juvenile phase in apple using transgenic approaches. Pp. 337–343 in *XXVI International Horticultural Congress: Biotechnology in Horticultural Crop Improvement: Achievements, Opportunities*. Acta Horticulturae 625. Korbek-Lo, Belgium: International Society for Horticultural Science.
- La Mantia, J., F. Unda, C.J. Douglas, S.D. Mansfield, and R. Hamelin. 2018. Overexpression of *AtGolS3* and *CsRFS* in poplar enhances ROS tolerance and represses defense response to leaf rust disease. *Tree Physiology* 38(3):457–470.

- Lachance, D., L.P. Hamel, F. Pelletier, J. Valéro, M. Bernier-Cardou, K. Chapman, K. Van Frankenhuyzen, and A. Séguin. 2007. Expression of a *Bacillus thuringiensis cry1Ab* gene in transgenic white spruce and its efficacy against the spruce budworm (*Choristoneura fumiferana*). *Tree Genetics & Genomes* 3(2):153–167.
- Le, V.Q., J. Belles Isles, M. Dusabenyagasani, and F.M. Tremblay. 2001. An improved procedure for production of white spruce (*Picea glauca*) transgenic plants using *Agrobacterium tumefaciens*. *Journal of Experimental Botany* 52(364):2089–2095.
- LeBlanc, P.M., R.C. Hamelin, and M. Filion. 2007. Alteration of soil rhizosphere communities following genetic transformation of white spruce. *Applied and Environmental Microbiology* 73(13):4128–4134.
- Levé, V., M.A. Lelu, L. Jouanin, D. Cornu, and G. Pilate. 1997. *Agrobacterium tumefaciens*-mediated transformation of hybrid larch (*Larix kaempferi* × *L. decidua*) and transgenic plant regeneration. *Plant Cell Reports* 16(10):680–685.
- Levé, V., E. Garin, K. Klimaszewska, and A. Séguin. 1999. Stable genetic transformation of white pine (*Pinus strobus* L.) after cocultivation of embryogenic tissues with *Agrobacterium tumefaciens*. *Molecular Breeding* 5(5):429–440.
- Liang, H., C.A. Maynard, R.D. Allen, and W.A. Powell. 2001. Increased *Septoria musiva* resistance in transgenic hybrid poplar leaves expressing a wheat oxalate oxidase gene. *Plant Molecular Biology* 45(6):619–629.
- Liu, X., and P.M. Pijut. 2010. *Agrobacterium*-mediated transformation of mature *Prunus serotina* (black cherry) and regeneration of transgenic shoots. *Plant Cell, Tissue and Organ Culture* 101(1):49–57.
- Mageroy, M.H., D. Lachance, S. Jancsik, G. Parent, A. Séguin, J. Mackay, and J. Bohlmann. 2017. *In vivo* function of *Pgβglu-1* in the release of acetophenones in white spruce. *PeerJ*, 5:e3535.
- Maleki, S.S., K. Mohammadi, and K. S. Ji. 2018. Study on factors influencing transformation efficiency in *Pinus massoniana* using *Agrobacterium tumefaciens*. *Plant Cell, Tissue and Organ Culture* 133(3):437–445.
- Maruyama, T.E., and Y. Hosoi. 2016. Somatic embryogenesis in Japanese black pine (*Pinus thunbergii* Parl.). Pp. 27–39 in *Somatic Embryogenesis in Ornamentals and Its Applications*, A. Mujib, ed. New Delhi: Springer.
- Maximova, S., C. Miller, G.A. De Mayolo, S. Pishak, A. Young, and M.J. Guiltinan. 2003. Stable transformation of *Theobroma cacao* L. and influence of matrix attachment regions on GFP expression. *Plant Cell Reports* 21(9):872–883.
- Maximova, S.N., J.P. Marelli, A. Young, S. Pishak, J.A. Verica, and M.J. Guiltinan. 2006. Over-expression of a cacao class I chitinase gene in *Theobroma cacao* L. enhances resistance against the pathogen, *Colletotrichum gloeosporioides*. *Planta* 224(4):740–749.
- McGranahan, G.H., C.A. Leslie, S.L. Uratsu, L.A. Martin, and A.M. Dandekar. 1988. *Agrobacterium*-mediated transformation of walnut somatic embryos and regeneration of transgenic plants. *Nature Biotechnology* 6(7):800–804.
- Newhouse, A.E., F. Schrod, H. Liang, C.A. Maynard, and W.A. Powell. 2007. Transgenic American elm shows reduced Dutch elm disease symptoms and normal mycorrhizal colonization. *Plant Cell Reports* 26(7):977–987.
- Newhouse, A.E., L.D. Polin-McGuigan, K.A. Baier, K.E. Valletta, W.H. Rottmann, T.J. Tschaplinski, C.A. Maynard, and W.A. Powell. 2014. Transgenic American chestnuts show enhanced blight resistance and transmit the trait to T1 progeny. *Plant Science* 228:88–97.
- Ning, K., S. Chen, H. Huang, J. Jiang, H. Yuan, and H. Li. 2017. Molecular characterization and expression analysis of the *SPL* gene family with *BpSPL9* transgenic lines found to confer tolerance to abiotic stress in *Betula platyphylla* Suk. *Plant Cell, Tissue and Organ Culture* 130(3):469–481.
- Noël, A., C. Levasseur, and A. Séguin. 2005. Enhanced resistance to fungal pathogens in forest trees by genetic transformation of black spruce and hybrid poplar with a *Trichoderma harzianum* endochitinase gene. *Physiological and Molecular Plant Pathology* 67(2):92–99.
- Nunes, S., L. Marum, N. Farinha, V.T. Pereira, T. Almeida, D. Sousa, N. Mano, J. Figueiredo, M.C. Dias, and C. Santos. 2018. Somatic embryogenesis of hybrid *Pinus elliottii* var. *elliottii* × *P. caribaea* var. *hondurensis* and ploidy assessment of somatic plants. *Plant Cell, Tissue and Organ Culture* 132(1):71–84.
- Oguchi, T., Y. Kashimura, M. Mimura, X. Yu, E. Matsunaga, K. Nanto, T. Shimada, A. Kikuchi, and K.N. Watanabe. 2014. A multi-year assessment of the environmental impact of transgenic *Eucalyptus* trees harboring a bacterial choline oxidase gene on biomass, precinct vegetation and the microbial community. *Transgenic Research* 23(5):767–777.
- Ouyang, L.J., and L.M. Li. 2016. Effects of an inducible *aiiA* gene on disease resistance in *Eucalyptus urophylla* × *Eucalyptus grandis*. *Transgenic Research* 25(4):441–452.
- Padilla, I.M., A. Golis, A. Gentile, C. Damiano, and R. Scorza. 2006. Evaluation of transformation in peach *Prunus persica* explants using green fluorescent protein (GFP) and beta-glucuronidase (GUS) reporter genes. *Plant Cell, Tissue and Organ Culture* 84(3):309–314.

- Palomo-Ríos, E., S. Cerezo, J.A. Mercado, and F. Pliego-Alfaro. 2017. *Agrobacterium*-mediated transformation of avocado (*Persea americana* Mill.) somatic embryos with fluorescent marker genes and optimization of transgenic plant recovery. *Plant Cell, Tissue and Organ Culture* 128(2):447–455.
- Pappinen, A., Y. Degefu, L. Syrjälä, K. Keinonen, and K. von Weissenberg. 2002. Transgenic silver birch (*Betula pendula*) expressing sugarbeet chitinase 4 shows enhanced resistance to *Pyrenopeziza betulicola*. *Plant Cell Reports* 20(11):1046–1051.
- Park, E.J., H.T. Kim, Y.I. Choi, C. Lee, V.P. Nguyen, H.W. Jeon, J.S. Cho, R. Funada, R.P. Pharis, L.V. Kurepin, and J.H. Ko. 2015. Overexpression of *gibberellin 20-oxidase1* from *Pinus densiflora* results in enhanced wood formation with gelatinous fiber development in a transgenic hybrid poplar. *Tree Physiology* 35(11):1264–1277.
- Pérez-Clemente, R.M., A. Pérez-Sanjuán, L. García-Férriz, J.P. Beltrán, and L.A. Cañas. 2005. Transgenic peach plants (*Prunus persica* L.) produced by genetic transformation of embryo sections using the green fluorescent protein (GFP) as an *in vivo* marker. *Molecular Breeding* 14(4):419–427.
- Polin, L.D., H. Liang, R.E. Rothrock, M. Nishii, D.L. Diehl, A.E. Newhouse, C.J. Nairn, W.A. Powell, and C.A. Maynard. 2006. *Agrobacterium*-mediated transformation of American chestnut (*Castanea dentata* (Marsh.) Borkh.) somatic embryos. *Plant Cell, Tissue and Organ Culture* 84(1):69–79.
- Qiao, G., J. Zhou, J. Jiang, Y. Sun, L. Pan, H. Song, J. Jiang, R. Zhuo, X. Wang, and Z. Sun. 2010. Transformation of *Liquidambar formosana* L. via *Agrobacterium tumefaciens* using a mannose selection system and recovery of salt tolerant lines. *Plant Cell, Tissue and Organ Culture* 102(2):163–170.
- Ramírez, A.M.H., T. de la Hoz Vasquez, T.M.O. Osorio, L.A. Garces, and A.I.U. Trujillo. 2018. Evaluation of the potential of regeneration of different Colombian and commercial genotypes of cocoa (*Theobroma cacao* L.) via somatic embryogenesis. *Scientia Horticulturae* 229:148–156.
- Ren, Y., J. Zhang, G. Wang, X. Liu, L. Li, J. Wang, and M. Yang. 2018. The relationship between insect resistance and tree age of transgenic triploid *Populus tomentosa* plants. *Frontiers in Plant Science* 9:53.
- Renying, Z., Q. Guirong, and S. Zongxiu. 2007. Transgene expression in Chinese sweetgum driven by the salt induced expressed promoter. *Plant Cell, Tissue and Organ Culture* 88(1):101–107.
- Sain, S.L., K.K. Oduro, and D.B. Furtek. 1994. Genetic transformation of cocoa leaf cells using *Agrobacterium tumefaciens*. *Plant Cell, Tissue and Organ Culture* 37(3):243–251.
- Scorza, R., M. Ravelonandro, A.M. Callahan, J.M. Cordts, M. Fuchs, J. Dunez, and D. Gonsalves. 1994. Transgenic plums (*Prunus domestica* L.) express the plum pox virus coat protein gene. *Plant Cell Reports* 14(1):18–22.
- Sheikh Beig Goharrizi, M.A., A. Dejahang, M. Tohidfar, A. Izadi Darbandi, N. Carillo, M.R. Hajirezaei, and K. Vahdati. 2016. *Agrobacterium* mediated transformation of somatic embryos of Persian walnut using *fld* gene for osmotic stress tolerance. *Journal on Agricultural Science and Technology* 18(2):423–435.
- Shim, D., S. Kim, Y.I. Choi, W.Y. Song, J. Park, E.S. Youk, S.C. Jeong, E. Martinoia, E.W. Noh, and Y. Lee. 2013. Transgenic poplar trees expressing yeast cadmium factor 1 exhibit the characteristics necessary for the phytoremediation of mine tailing soil. *Chemosphere* 90(4):1478–1486.
- Sidorova, T., A. Pushin, D. Miroshnichenko, and S. Dolgov. 2018. Generation of transgenic rootstock plum (*Prunus pumila* L. × *P. salicina* Lindl.) × (*P. cerasifera* Ehrh.) using hairpin-RNA construct for resistance to the plum pox virus. *Agronomy* 8(1):2.
- Silva, T.E., L.C. Cidade, F.C. Alvim, J.C. Cascardo, and M.G. Costa. 2009. Studies on genetic transformation of *Theobroma cacao* L.: Evaluation of different polyamines and antibiotics on somatic embryogenesis and the efficiency of *uidA* gene transfer by *Agrobacterium tumefaciens*. *Plant Cell, Tissue and Organ Culture* 99(3):287–298.
- Song, G.Q., and K.C. Sink. 2006. Transformation of Montmorency sour cherry (*Prunus cerasus* L.) and Gisela 6 (*P. cerasus* × *P. canescens*) cherry rootstock mediated by *Agrobacterium tumefaciens*. *Plant Cell Reports* 25(2):117–123.
- Song, G.Q., K.C. Sink, A.E. Walworth, M.A. Cook, R.F. Allison, and G.A. Lang. 2013. Engineering cherry rootstocks with resistance to *Prunus* necrotic ring spot virus through RNAi mediated silencing. *Plant Biotechnology Journal* 11(6):702–708.
- Sullivan, J., and L.M. Lagrimini. 1993. Transformation of *Liquidambar styraciflua* using *Agrobacterium tumefaciens*. *Plant Cell Reports* 12(6):303–306.
- Sun, X., P. Wang, X. Jia, L. Huo, R. Che, and F. Ma. 2018. Improvement of drought tolerance by overexpressing *MdATG18a* is mediated by modified antioxidant system and activated autophagy in transgenic apple. *Plant Biotechnology Journal* 16(2):545–557.
- Tang, W., and Y. Tian. 2003. Transgenic loblolly pine (*Pinus taeda* L.) plants expressing a modified δ endotoxin gene of *Bacillus thuringiensis* with enhanced resistance to *Dendrolimus punctatus* Walker and *Crypytholea formosicola* Staud. *Journal of Experimental Botany* 54(383):835–844.

- Tang, W., B. Xiao, and Y. Fei. 2014. Slash pine genetic transformation through embryo cocultivation with *A. tumefaciens* and transgenic plant regeneration. *In Vitro Cellular & Developmental Biology-Plant* 50(2):199–209.
- Vahdati, K., J.R. McKenna, A.M. Dandekar, C.A. Leslie, S.L. Uratsu, W.P. Hackett, P. Negri, and G.H. McGranahan. 2002. Rooting and other characteristics of a transgenic walnut hybrid (*Juglans hindsii* × *J. regia*) rootstock expressing *rolABC*. *Journal of the American Horticultural Society* 127(5):724–728.
- Vardi, A., S. Bleichman, and D. Aviv. 1990. Genetic transformation of *Citrus* protoplasts and regeneration of transgenic plants. *Plant Science* 69(2):199–206.
- Wagner, A., L. Phillips, R.D. Narayan, J.M. Moody, and B. Geddes. 2005. Gene silencing studies in the gymnosperm species *Pinus radiata*. *Plant Cell Reports* 24(2):95–102.
- Wagner, A., Y. Tobimatsu, L. Phillips, H. Flint, K. Torr, L. Donaldson, L. Pears, and J. Ralph. 2011. *CCoAOMT* suppression modifies lignin composition in *Pinus radiata*. *Plant Journal* 67(1):119–129.
- Wagner, A., Y. Tobimatsu, G. Goeminne, L. Phillips, H. Flint, D. Steward, K. Torr, L. Donaldson, W. Boerjan, and J. Ralph. 2013. Suppression of *CCR* impacts metabolite profile and cell wall composition in *Pinus radiata* tracheary elements. *Plant Molecular Biology* 81(1–2):105–117.
- Wagner, A., Y. Tobimatsu, L. Phillips, H. Flint, B. Geddes, F. Lu, and J. Ralph. 2015. Syringyl lignin production in conifers: Proof of concept in a Pine tracheary element system. *Proceedings of the National Academy of Sciences of the United States of America* 12(19):6218–6223.
- Walawage, S.L., C.A. Leslie, M.A. Escobar, and A.M. Dandekar. 2014. *Agrobacterium tumefaciens*-mediated transformation of walnut (*Juglans regia*). *Plant Physiology* 4(19):e1258.
- Wang, Q.J., H. Sun, Q.L. Dong, T.Y. Sun, Z.X. Jin, Y.J. Hao, and Y.X. Yao. 2016. The enhancement of tolerance to salt and cold stresses by modifying the redox state and salicylic acid content via the cytosolic malate dehydrogenase gene in transgenic apple plants. *Plant Biotechnology Journal* 14(10):1986–1997.
- Wang, Y., and P.M. Pijut. 2014. *Agrobacterium*-mediated transformation of black cherry for flowering control and insect resistance. *Plant Cell, Tissue and Organ Culture* 119(1):107–116.
- Wu, N.F., Q. Sun, B. Yao, Y.L. Fan, H.Y. Rao, M.R. Huang, and M.X. Wang. 2000. Insect-resistant transgenic poplar expressing *AaIT* gene. *Chinese Journal of Biotechnology* 16(2):129–133.
- Yang, J., K. Li, C. Li, J. Li, B. Zhao, W. Zheng, Y. Gao, and C. Li. 2018. In vitro anther culture and *Agrobacterium*-mediated transformation of the *AP1* gene from *Salix integra* Linn. in haploid poplar (*Populus simonii* × *P. nigra*). *Journal of Forestry Research* 29(2):321–330.
- Yu, X., A. Kikuchi, T. Shimazaki, A. Yamada, Y. Ozeki, E. Matsunaga, H. Ebinuma, and K.N. Watanabe. 2013. Assessment of the salt tolerance and environmental biosafety of *Eucalyptus camaldulensis* harboring a *mangrin* transgene. *Journal of Plant Research* 126(1):141–150.
- Zaragoza, C., J. Munoz-Bertomeu, and I. Arrillaga. 2004. Regeneration of herbicide-tolerant black locust transgenic plants by SAAT. *Plant Cell Reports* 22(11):832–838.
- Zeng, F., Y. Zhan, N. Nan, Y. Xin, F. Qi, and C. Yang. 2009. Expression of *bgt* gene in transgenic birch (*Betula platyphylla* Suk.). *African Journal of Biotechnology* 8(15):3392–3398.
- Zhang, Q., S. Lin, Y. Lin, Z. Zhang, H. Liu, Y. Zou, and Z. Wang. 2004. Identification of *CpTI* gene integration for 2-year-old transgenic poplars at DNA level. *Forestry Studies in China* 6(3):15–19.
- Zhou, X., T.B. Jacobs, L.J. Xue, S.A. Harding, and C.J. Tsai. 2015. Exploiting SNP s for biallelic CRISPR mutations in the outcrossing woody perennial *Populus* reveals 4 coumarate: CoA ligase specificity and redundancy. *New Phytologist* 208(2):298–301.
- Zong, X., Q. Chen, M.A. Nagaty, Y. Kang, G. Lang, and G.Q. Song. 2018. Adventitious shoot regeneration and *Agrobacterium tumefaciens*-mediated transformation of leaf explants of sweet cherry (*Prunus avium* L.). *Journal of Horticultural Science and Biotechnology*: 1–8.
- Zuo, L., R. Yang, Z. Zhen, J. Liu, L. Huang, and M. Yang. 2018. A 5-year field study showed no apparent effect of the *Bt* transgenic 741 poplar on the arthropod community and soil bacterial diversity. *Scientific Reports* 8(1):1956.

Appendix D

Chronological Summary of Studies Empirically Examining Public and Other Stakeholder Responses to the Use of Biotechnology in Trees and Forests

Citation	Main Focus	Study Location	Methods	Main Findings
Friedman and Foster (1997)	Stakeholder concerns about genetic diversity and tree improvement on public land	United States	Informal qualitative interviews with U.S. Forest Service employees	Concerns about risks of changes in the genetics of future trees include reduction of genetic diversity, loss of adaptation, and changes in other ecosystem components from the directed selection of trees
Neumann et al. (2007)	Differences between expert and public perceptions of plantation forestry, specifically hybrid poplar plantations	Canada	Qualitative interviews with key informants ($n = 31$)	Framing identity, trust, and economic competition are important for an overall assessment of community perceptions of hybrid poplar plantations
Strauss et al. (2009)	Degree that the knowledgeable scientific community believes regulatory requirements present a significant impediment to field research and commercial development of genetically modified trees, and why	United States and Canada	Online and follow-up telephone surveys of scientists in university, government, and the private sector ($n = 90$)	A large majority (78%) of respondents agreed with the statement that “regulatory requirements pose a substantial obstacle to field research on genetically engineered trees.” When the same statement was provided, but with respect to “commercial development and breeding with genetically engineered trees,” the majority grew stronger with 81% agreeing. In addition, 72% believed “containment requirements have an adverse impact on the continued research and commercial development” of these trees and 93% believed “a system that provided different containment requirements during research for different kinds of genes” would significantly reduce regulatory burdens. Primary constraints to broader application of genetically engineered trees were “regulatory costs and uncertainties at the commercial release level” (66%), “legal and liability risks from unintended release” (60%), and “high costs of field research” with these trees (59%)
Connor and Siegrist (2010)	Factors influencing perceptions of several different gene technologies, including genetic modification of trees to grow faster to produce more paper/wood	Switzerland	Mail survey of a random sample of German speaking residents of Switzerland ($n = 830$)	Medical applications of gene technology were more acceptable and perceived to have more benefits and less risk than nonmedical applications such modification of trees to produce more paper / wood. Benefits, risks, and trust predicted acceptance
Tsourgiannis et al. (2013)	Consumer attitudes and purchasing behavior toward wood products that could be derived from transgenic plantations, their personal characteristics, and their attitude toward establishing these plantations	Greece	Onsite survey in supermarkets and malls ($n = 418$), although analyses were conducted only on consumers who declared they would be willing to buy wood products from genetically modified forest trees ($n = 231$)	Main factors affecting consumer purchasing behavior towards those products are promotion/marketing issues (e.g., origin, attractiveness), product features (e.g., quality, brand name), and labelling. Perceived benefits of establishing forest transgenic plantations include increased job flexibility, reduced production cost, increases in farmer income, and reduction of production losses. Environmental issues that may arise from adoption of transgenic forest plantations were not as important as these economic issues to the consumers

Hajjar et al. (2014)	Acceptance of a range of reforestation strategies (some revolving around biotechnology) that could be used for helping western Canada's forests adapt to future climate change	Western Canada	Online surveys of residents ($n = 1544$) and leaders of forestry communities ($n = 37$) in Alberta and British Columbia	The strategy "plant seedlings grown from seeds that are genetically engineered (GMOs) to grow well in the climate conditions expected to occur in the near future" was less acceptable than breeding and assisted migration strategies, but was still acceptable among approximately 50% of the public and 30% of forestry leaders, and was more acceptable than doing nothing. Acceptance changed for many respondents after being told the strategy would create positive benefits or negative risks and other outcomes (e.g., community socioeconomics, forest aesthetics, outbreaks of pests, diseases, and fire)
Hajjar and Kozak (2015)	Predictors of acceptance of several reforestation strategies (some focused on biotechnology) that could be used for helping western Canada's forests adapt to climate change	Western Canada	Online survey of residents ($n = 1544$) in Alberta and British Columbia	Approximately 50% of the public accepted the strategy "plant seedlings grown from seeds that are genetically engineered (GMOs) to grow well in the climate conditions expected to occur in the near future" and this was influenced by skepticism, trust in decision makers, risks/threats from technology, risks and ethics associated with manipulating nature, age, and being male
Nonić et al. (2015)	Impact of education level and background knowledge and perceptions of risks and benefits on attitudes toward acceptance of the commercial use of genetically modified trees and their final products	Serbia	Onsite survey of students at two different universities ($n = 400$)	Over 70% knew what a genetically modified tree was, but commercial application and final products of these trees were less known. Students with more years of education were more likely to know about these trees and their uses. Genetic modifications aimed at enhancing the resistance of trees to diseases was the most acceptable. Perceived benefits of these trees included less need for pesticides and greater tree productivity. Perceived risks included loss of biodiversity, need for more broad spectrum herbicides, and vulnerability to viral diseases. The majority of respondents agreed with commercial planting of transgenic forest crops, were willing to purchase products from these trees, and thought labeling of these products should be required
Tsourgiannis et al. (2015)	Attitudes and potential purchasing behavior of Greek consumers toward products derived from transgenic forest tree plantations. Demographic characteristics and responses toward the establishment of these plantations is also investigated	Greece	Onsite survey in supermarkets and malls ($n = 418$)	Four groups of consumers showing similar potential purchasing behavior toward products from transgenic forest trees were identified—those interested in: (a) the quality of products (12%), (b) lower prices (30%), (c) curiosity and labeling issues (35%), and (d) health safety issues and environmental impacts (23%). Perceived benefits of establishing transgenic forest plantations included more job opportunities, increased farmer income, improved production of biomass, and reduced production cost and output losses. Risks included negative impacts on wild native species, the biodiversity of ecosystems, and human health. There were some demographic differences, as the group interested in the quality of products was older, less educated, and did not have children, whereas the other groups were younger, more educated, and had children

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Citation	Main Focus	Study Location	Methods	Main Findings
Kazana et al. (2015, 2016)	Young people's knowledge about transgenic forest trees, concerns regarding cultivation of these trees, and attitudes toward the use of transgenic forest trees in plantations	15 European and non-European countries (Argentina, Australia, Israel)	Onsite survey of university students in each country ($n = 1868$)	More than 60% of students knew the meaning of forest transgenic trees. However, most did not know whether they were grown commercially. The majority of respondents approved of growing transgenic trees in plantations (56–93%), using labels to indicate final products originated from genetically modified trees (77–98%), and make labels mandatory (73–99%). Potential benefits of transgenic tree plantations that were rated as important in at least half of the countries were use of fewer chemicals (insecticides, pesticides, herbicides) and less energy, harvesting a smaller number of trees for consumption, restoring soils, and increasing tree productivity. The largest risks were loss of biodiversity due to possible gene flow between transgenic plantations and wild forests, increased herbicide use and resistance, and vulnerability to other tree diseases. More than half of respondents, however, were unable to specify benefits and risks, indicating low levels of specific knowledge
Fuller et al. (2016)	Acceptance of various tree health management methods (including “biological control,” and how opinions about woodland functions, concern and awareness of pests and diseases, and demographics influence acceptance of these methods	United Kingdom	Online survey from a panel of residents ($n = 2208$)	The majority of respondents (74%) were “concerned” or “very concerned” about the threat of pests and diseases to trees. In total, 66% of respondents considered “biological control” to be acceptable for managing tree pests and diseases. Only “felling only affected trees” was more acceptable. Acceptance increased when the importance of environmental functions were high
Needham et al. (2016)	Measure various cognitions (e.g., attitudes, norms, behavioral intentions, risk, benefits) in response to several possible biotechnological (e.g., genetic modification) and non-biotechnological (e.g., conventional breeding) interventions for addressing forest health threats such as chestnut blight and climate change. Examine the effect of scientific information and messaging on these cognitions	United States	Mail surveys of US residents ($n = 278$) and interest groups (e.g., scientists, companies, agencies, non-governmental organizations; $n = 195$), onsite survey of students in seven universities ($n = 604$), and online survey of Qualtrics panel members ($n = 528$)	Attitudes showed less acceptance for genetic modification compared to tree breeding and traditional forest management, but genetic modification was more acceptable for addressing a pathogen such as chestnut blight (68%) than for climate change (53%) or to increase forest growth/productivity (55%). Changing genes in American chestnut trees (69%) and adding genes from bread wheat (i.e., <i>OxO</i> gene; 61%) were more acceptable than breeding with non-native species such as Asian chestnuts (60%) and adding genes from distantly related organisms (53%). Value orientations, factual knowledge, trust, gender, perceived risks and benefits toward the environment, and residential proximity to forests all influenced support of genetic modification for addressing chestnut blight. This support, however, is sensitive to informational messages and vulnerable to persuasion campaigns, as it dropped dramatically (from 75–83% down to 40–44%) as soon as messages provided any negative/anti arguments (i.e., pejorative language) about this topic
Nilausen et al. (2016)	Perceived acceptability of implementing marker-assisted selection (MAS; flags desired traits on the genome to reduce the breeding cycle and more accurately and efficiently selecting for improved qualities)	Canada	Qualitative interviews and quantitative pre and post video questionnaires (to ensure knowledge) to small sample ($n = 25$) of four groups (government, industry, environmental NGOs)	The video improved knowledge about MAS. Government (78%) and industry (100%) held positive attitudes toward MAS, supporting its use and continued research. Environmental NGOs (50%) and First Nations (17%) attitudes were far less positive. Government and industry were more likely to explain the difference between genetic modification and MAS, and emphasize the improved forest resiliency and industry-specific traits. Environmental NGOs were concerned about risks such as a tree's ability to adapt to climate change and its

			[non-governmental organizations], First Nations)	reduced genetic diversity, but thought benefits may include ability to reduce pressure on wild forests. First Nations were concerned about how their community and/or elders would respond, but mentioned benefits such as greater carbon sequestration capacity
Tsourgiannis et al. (2016)	Consumer attitudes and purchasing behavior toward wood products that could be derived from transgenic plantations, their personal characteristics, and their attitude toward establishing these plantations	Greece	Onsite survey in supermarkets and malls ($n = 418$)	Respondents were segmented according to their buying behavior for three forest product categories of transgenic origin: (a) paper products, (b) wood products, and (c) woody biomass energy products. Marketing issues (e.g., origin, attractiveness) and product features (e.g., quality, brand name) influenced buying behavior for all three groups. Health and safety issues only influenced purchasers of woody biomass energy products. Labeling and certification were important for wood products and woody biomass energy products. Environmental impacts were important for those purchasing paper products.
Jepson and Arakelyan (2017a)	Public acceptance of various potential strategies to deal with ash dieback and develop disease tolerant ash trees, ranging from traditional tree breeding to genetic modification. Predictors of this acceptance were also measured (e.g., demographics, concern, support of genetically modified foods)	United Kingdom	Onsite survey of 1,152 attendees of three events attracting publics interested in the countryside: landowners and land managers, naturalists, and gardeners	Respondents care about the issue, want an active response (i.e., doing nothing was least acceptable), and prefer traditional or accelerated breeding solutions over genetic modification. Creating a disease tolerant ash tree using trans-genetics was the least acceptable option; more respondents supported a cisgenics option and this increased to 54% when informed of the time scale (<10 years for achieving outcome). In total, 38% approved of genetically modified ash trees being planted in natural woodlands, and 60% supported them in forestry plantations. Type of event attended, views on ash dieback, public say on decision making, education, age (younger more supportive), and attitude to genetically modified food all had significant effects on these attitudes to genetically modified ash trees
Jepson and Arakelyan (2017b)	Public preferences for seven potential options for dealing with ash dieback, ranging from traditional tree breeding to genetic modification, with approximate timescales given for the implementation of each option. Predictors were also measured (e.g., demographics, concern, support of genetically modified foods)	United Kingdom	Online survey using the YouGov list ($n = 2,036$) and weighted to be representative of adult residents in the United Kingdom	Breeding native tolerant ash, planting different species, and accelerated breeding were most preferred. Using genetically modified techniques were preferred by 27% of respondents, with greater support for this in urban areas and plantations. No action and planting and breeding non-native ash were least preferred. Younger, more educated, and male respondents were more supportive of genetically modified techniques. The largest percentage of respondents (43%) saw no difference between genetic modification of trees versus food, but 20% said modification of trees is less acceptable because it involves tampering with nature. Knowledge about plant science, however, was low
Peterson St-Laurent et al. (2018)	Predictors of acceptance of several reforestation strategies (one that focused on biotechnology) that could be used for helping western Canada's forests adapt to climate change	Western Canada	Online survey of residents ($n = 1,923$) in British Columbia	Only 25% of the public supported the strategy "plant seedlings from seeds that are genetically modified to be better adapted to anticipated future climatic conditions" and only 16% were in favor of this intervention from an ethical standpoint. Support was influenced by anthropocentric value orientations, knowledge of forestry, preferred economic outcomes, trust in decision makers, age, being male, and employment in the forest industry.

REFERENCES

- Connor, M., and M. Siegrist. 2010. Factors influencing people's acceptance of gene technology: The role of knowledge, health expectations, naturalness, and social trust. *Science Communication* 32(4):514–538.
- Friedman, S.T., and G.S. Foster. 1997. Forest genetics on federal lands in the United States: Public concerns and policy responses. *Canadian Journal of Forest Research* 27(3):401–408.
- Fuller, L., M. Marzano, A. Peace, and C.P. Quine. 2016. Public acceptance of tree health management: Results of a national survey in the UK. *Environmental Science and Policy* 59(1):18–25.
- Hajjar, R., and R.A. Kozak. 2015. Exploring public perceptions of forest adaptation strategies in Western Canada: Implications for policymakers. *Forest Policy and Economics* 61:59–69.
- Hajjar, R., E. McGuigan, M. Moshofsky, and R.A. Kozak. 2014. Opinions on strategies for forest adaptation to future climate conditions in western Canada: Surveys of the general public and leaders of forest-dependent communities. *Canadian Journal of Forest Research* 44(12):1525–1533.
- Jepson, P.R., and I. Arakelyan. 2017a. Developing publicly acceptable tree health policy: Public perceptions of tree-breeding solutions to ash dieback among interested publics in the UK. *Forest Policy and Economics* 80:167–177.
- Jepson, P., and I. Arakelyan. 2017b. Exploring public perceptions of solutions to tree diseases in the UK: Implications for policy-makers. *Environmental Science and Policy* 76:70–77.
- Kazana, V., L. Tsourgiannis, V. Iakovoglou, C. Stamatiou, A. Alexandrov, S. Araújo, S. Bogdan, G. Božič, R. Brus, G. Bossinger, A. Boutsimea, N. Celepirović, H. Cvrčková, M. Fladung, M. Ivanković, A. Kazaklis, P. Koutsona, Z. Luthar, P. Máchová, J. Malá, K. Mara, M. Mataruga, J. Moravcikova, D. Paffetti, J. Paiva, D. Raptis, C. Sanchez, S. Sharry, T. Salaj, M. Šijačić-Nikolić, N. Tel-Zur, I. Tsvetkov, C. Vettori, and N. Vidal. 2015. Public attitudes towards the use of transgenic forest trees: A cross-country pilot survey. *iForest* 9:344–353.
- Kazana, V., L. Tsourgiannis, V. Iakovoglou, C. Stamatiou, A. Alexandrov, S. Araújo, S. Bogdan, G. Božič, R. Brus, G. Bossinger, A. Boutsimea, N. Celepirović, H. Cvrčková, M. Fladung, M. Ivanković, A. Kazaklis, P. Koutsona, Z. Luthar, P. Máchová, J. Malá, K. Mara, M. Mataruga, J. Moravcikova, D. Paffetti, J. Paiva, D. Raptis, C. Sanchez, S. Sharry, T. Salaj, M. Šijačić-Nikolić, N. Tel-Zur, I. Tsvetkov, C. Vettori, and N. Vidal. 2016. Public knowledge and perceptions of safety issues towards the use of genetically modified forest trees: A cross-country pilot survey. Pp. 223–244 in *Biosafety of Forest Transgenic Trees: Improving the Scientific Basis for Safe Tree Development and Implementation of EU Policy Directives*, C. Vettori, F. Gallardo, H. Häggman, V. Kazana, F. Migliacci, G. Pilate, and M. Fladung, eds. Dordrecht, Netherlands: Springer.
- Needham, M., G. Howe, and J. Petit. 2016. *Forest Health Biotechnologies: What Are the Drivers of Public Acceptance? Interim report and preliminary findings for the Forest Health Initiative and U.S. Endowment for Forestry and Communities*. Available at <https://www.foresthealthinitiative>.
- Neumann, P.D., N.T. Krogman, and B.R. Thomas. 2007. Public perceptions of hybrid poplar plantations: Trees as an alternative crop. *International Journal of Biotechnology* 9(5):468–483.
- Nilausen, C., N. Gélinas, and G. Bull. 2016. Perceived acceptability of implementing marker-assisted selection in the forests of British Columbia. *Forests* 7(11):286.
- Nonić, M., U. Radojević, J. Milovanović, M. Perović, and M. Šijačić-Nikolić. 2015. Comparative analysis of students' attitudes toward implementation of genetically modified trees in Serbia. *iForest* 8:714–718.
- Peterson St-Laurent, G., S. Hagerman, and R. Kozak. 2018. What risks matter? Public views about assisted migration and other climate-adaptive reforestation strategies. *Climatic Change* 151(3–4):573–587.
- Strauss, S.H., M. Schmitt, and R. Sedjo. 2009. Forest scientist views of regulatory obstacles to research and development of transgenic forest biotechnology. *Journal of Forestry* 107(7):350–357.
- Tsourgiannis, L., V. Kazana, A. Karasavoglou, M. Nikolaidis, G. Florou, and P. Polychronidou. 2013. Exploring consumers' attitudes towards wood products that could be derived from transgenic plantations in Greece. *Procedia Technology* 8:554–560.
- Tsourgiannis, L., V. Kazana, and V. Iakovoglou. 2015. Exploring the potential behavior of consumers towards transgenic forest products: The Greek experience. *iForest* 8:707–713.
- Tsourgiannis, L., V. Kazana, and V. Iakovoglou. 2016. A comparative analysis of consumers' potential purchasing behaviour towards transgenic-derived forest products: The Greek case. Pp. 245–260 in *Biosafety of Forest Transgenic Trees: Improving the Scientific Basis for Safe Tree Development and Implementation of EU Policy Directives*, C. Vettori, F. Gallardo, H. Häggman, V. Kazana, F. Migliacci, G. Pilate, and M. Fladung, eds. Dordrecht, Netherlands: Springer.